Annals
of the
Missouri Botanical Garden

Vol. 44 NOVEMBER, 1957 No. 4

MORPHOLOGICAL COMPLEXES IN HOPS (*HUMULUS LUPULUS* L.) WITH SPECIAL REFERENCE TO THE AMERICAN RACE[1]

EDWARD L. DAVIS[2]

The genus *Humulus* cannot be treated taxonomically as can a plant known exclusively in the wild. Unlike many cultivated plants, hops are fairly easily established as escapes from cultivation, and the distinction between wild and cultivated hops is not easily drawn. One may be certain that the natural distribution of hops has been greatly modified by man. Yet hops cannot be studied only as cultivated plants if the origin and relations of the various cultivated varieties are to be understood. The record of hop varieties is so incomplete that the history of many of the most important cultivated varieties is not known with certainty. The relationships between these varieties, as well as the more fundamental and difficult question of the origin of cultivated hops, cannot be determined without a close examination of wild-growing hops. It has therefore been necessary to attempt a simultaneous study of cultivated and wild forms, though in the following paper the emphasis will be given only to the American hops. A later publication will consider the cultivated varieties of the world in more detail.

Hops have found many uses, in addition to that of flavoring beer, which have led to their cultivation over a wide geographical area. Sometimes the use has been such that hops have been cultivated in small gardens rather than in large fields. Many of the early medicinal uses were summarized by John Parkinson (1640) who noted that the young buds served "to open obstructions of liver and spleene, to clense the blood, to loosen the belly", and in clensing the blood hops help to cure "all manners of scabes, itch, ringwormes and spreading sores." Various parts of the plant were used: "seeds in powder taken in drink killeth the worm in the body; the juice of the leaves dropped into the ears clenseth the corrupt sores; a syrup, made of the juice and sugar cureth those that have the

[1] An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University and submitted as part of a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] University of Massachusetts, Amherst, Mass.

yellow jaundice, easeth headache that cometh of heate, and temper the heate both of the liver and stomach." Hops have found additional medicinal use in poultices for swellings and tumors, for relieving pain of gout and rheumatism, and for calming nervous irritation (Simmonds, 1877). They were widely regarded as having a soporific effect, and pillows were stuffed with them. This practice attracted attention when Dr. Willis, in 1787, prescribed the use of a hop pillow for George III (Johnson, 1867). Morgan (1952) suggested that the hop-screened front porches of rural homes in the northern part of the United States served to lull farm folks to sleep after a hard day's work. Dr. Edgar Anderson recalls the practice in upper New York State and Michigan during the nineteenth century of planting hop vines outside the bedroom window.

For these medicinal uses the quantity of hops required was not great, and sufficient was easily grown in the family garden. Such small scale, but widely practiced, cultivation has given man an unusually fine opportunity to alter drastically the natural distribution of this plant. According to De Candolle (1883), the hop is native to Europe and Asia, from England and Sweden as far south as the mountains of the Mediterranean basin, and in Asia as far as Damascus, the south of the Caspian Sea and eastern Siberia, and it is not native to India and China. Nuttall (1847) considered it certainly indigenous to western United States, but the following letter by Asa Gray[3] in answer to a request for American wild hops, does not give any suggestion that they are to be found in the East:

> There is hardly a doubt that all the hops raised in North America are originally from plants introduced from Europe. If these will answer the purpose, it would be easy to have a sufficient quantity of American-grown hops sent to London; still easier to obtain them in the London market. But if hops from the native *Humulus Lupulus* are desired, this will not be easy. They grow, indeed, in a scattered way along the banks of certain streams, from Canada west to New Mexico, probably also in Arizona, but, if there, certainly in the secluded mountains only, and being dioecious, they can only now and then be found in fruit. I have myself seen the plant growing wild, but never in such a way that I could have gathered a pound of dried hops.

There is morphological and cytological evidence, presented below, for the existence of an American race of hop, quite distinct, though in minor details, from the European hop.

Nomenclature

The genus *Humulus* has been placed variously in the families Moraceae,[4] the Urticaceae,[5] and the Cannabineae.[6] The question of the organization and size of families is beyond the scope of this treatment, and I am following Rendle[7] (1952) in considering it a member of the Cannabinaceae, with the closely allied hemp.

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[3] In Am. Druggist 15:111. 1886.
[4] Engler, K., und Prantl, K. Nat. Pflanzenfam. III[1]:96. 1888.
[5] Bentham, G., and Hooker, J. D. Genera Plantarum 3:356–357. 1883.
[6] De Candolle, A. Prodr. 16[1]:28–31. 1869.
[7] Rendle, A. B. The classification of flowering plants 2:56–58. 1952.

Linnaeus, in the first edition of the 'Species Plantarum'[8] listed a single species *H. lupulus* L. Over one hundred years later, A. De Candolle, 1869, in his treatment of the Cannbineae, included three species in the genus: *H. lupulus* L., *H. cordifolius* Miq., and *H. japonicus* Sieb. & Zucc. He did, however, question the validity of *H. cordifolius* Miq.

H. lupulus and *H. japonicus* are very distinct species. The former is a perennial, with numerous lupulin glands upon the bracts and bracteoles of the cones, and the lower surface of the leaves, and with a diploid chromosome number of 20 (Ono, 1955, Sinoto, 1929, Winge, 1929). *H. japonicus* is an annual, with lupulin glands rare or absent, and a 2 N number of 17 in the male, 16 in the female (Kihara, 1929, Winge, 1929, Sinoto, 1929). *H. cordifolius* Miq. will be considered on a following page.

After 1753, the following names were used for the European hop in disregard of the prior Linnaean name:

Lupulus scandens Lam. Fl. Fr. 2:217. 1778.
L. communis Gaertn. Fruct. 1:358. *t. 75*. 1788.
L. amarus Gilib. Exercit. 2:451. 1792.
H. volubilis Salisb. Prod. 176. 1796.
H. vulgaris Gilib. Hist. Pl. Europ. 2:343. 1798.
H. aculeatus Nutt. in Jour. Acad. Philad. N. S. 1:182. 1847.

Nuttall (1847) considered that the hop native to western United States was distinct from the European *H. lupulus*. He established *H. americanus* from a collection made by Dr. Gambel in New Mexico. His description and comments follow:

> *H. americanus:* Leaves 3 to 5 lobed, the upper sometimes entire, inner divisions lanceolate-acuminate, denticulate along the apex; scales of the cone ovate, acute, the lower ones acuminate.
> I have ventured, as I think, upon sufficient grounds, to separate the American from the European hop, found as it is in the uncultivated interior of the continent beyond the reach of inhabitants, our plants must necessarily be indigenous. I have compared the present with the foreign plant with some attention, and I can in all cases readily distinguish them by their foliage. In the American plant, whatever be the other variations of the leaf, the attenuated points are denticulated nearly to the extremity. In the European the summit of the leaf is abruptly toothed. In the native plant, the male flowers appear to be smaller, and the scales of the cone are likewise acuminate. In some specimens, as in the European plant, the upper leaves are simply cordate, and entire, but in all cases the denticulations are smaller, and more numerous.

This separation was not universally accepted, and Asa Gray retained but the single species *H. lupulus* L. in the revised edition of his 'Manual'.[9] Still later, other attempts were made to establish an American segregate. Nelson and Cockerell[10] proposed the variety *H. lupulus* L. var. *neomexicanus*. Again the type was from the Southwest (Beulah, New Mexico). The lateness of the date should not pass

[8] Sp. Pl. p. 1028. 1753.
[9] Man. Bot. North. U. S. p. 400. 1857.
[10] Proc. Biol. Soc. Wash. 16:45. 1903.

unnoticed. In the fifty years since Nuttall's collection there was much opportunity for cultivated forms to become established as escapes.

There is absolutely nothing in their descriptions which would make it possible to differentiate between the American variety and *H. lupulus* L. of Europe, except the geographical location. The acuminate fruiting bract used to set off the variety occurs widely among European hops, both wild and cultivated.

Rydberg, in the 'Flora of Colorado',[11] lists the single species *H. lupulus* L. *neomexicanus* Cockerell for the Rocky Mountains. He says: "The native hops of the Rocky Mountain region has deeper divided leaves and more sharply acuminate bracts than the cultivated variety. It grows along streams from Wyo. to Utah, N. M. and Ariz."

This represents the first suggestion that the American type may be identified by the divisions of the leaf. By 1917, Rydberg had raised the variety to the species level.[12] The lobing of the leaves in the inflorescence, which he used in the key, is highly variable and not of any taxonomic significance.

At best, the descriptions and keys of the above authors permit the classification of some herbarium specimens into one or another species or variety. They do not establish a type found predominately in North America and separated from all European forms. The confusion is summarized by Fernald[13]: "The native plant sometimes called *H. americanus* Nutt., *H. lupulus* var. *neomexicanus* Nels. & Cockerell and *H. neomexicanus* (Nels. & Cockerell) Rydb.; its characters evasive."

Extensive comparisons of European and American hops bring out, above all, their great similarity. It is possible to differentiate between the European and American type on the basis of a complex of characters, but only when cone and leaf material is carefully collected. Consequently, I consider that for the present it is advisable to retain the name *H. lupulus* L. for the wild perennial hop of Europe and America.

The annual *H. japonicus* Sieb. & Zucc.[14] is a very distinct species which, because of the small number of lupulin glands, has never been used in the making of beer. Native to Asia, it is now widely scattered in North America as an adventive weed. Merrill[15] proposed using the name *H. scandens* (Lour.) Merr. for *H. japonicus* on the following grounds:

> Loureiro's poor description [of *Antidesma scandens* Lour. 1790], based upon a nearly glabrous form for which he saw only staminate specimens, applies unmistakably to the species currently known as *H. japonicus* Sieb. & Zucc. No other known Kwangtung species in any family remotely conforms to the characters indicated by Loureiro.

Loureiro's description is extremely vague, and I am following Fernald in retaining *H. japonicus* Sieb. & Zucc.

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[11] Fl. Colo. p. 100. 1906.
[12] Fl. Rocky Mts. & Adj. Plains, p. 408. 1917.
[13] Gray's Man. Bot. p. 556. 8th ed. by M. L. Fernald. 1950.
[14] Fl. Jap. Fam. Nat. 2:89 (Abh. K. Akad. Münch. math.-nat. Kl. 4^2:213. 1846.
[15] Merrill, E. D. A commentary on Loureiro's "Flora Cochinchinensis." Trans. Amer. Phil. Soc. n. s. 24^2:138. 1935.

Maximowicz[16] makes reference to his reduction of *Humulus cordifolius* Miq. to a variety, noting that De Candolle had erred in placing it near *H. japonicus* in his key on the grounds that lupulin glands were absent on the bracts and bracteoles. On the contrary, Maximowicz emphasizes the presence of such glands by concluding that it is as suitable for use in brewing as is the European hop. Miquel's description[17] is very incomplete, being based only upon female material, and Maximowicz did not clarify the situation. Hance[18] provided the first description of the male plant, but the description contains nothing which could be used to separate it from *H. lupulus*. Furthermore, an examination of specimens from Maximowicz's collection shows it to be identical with the European hop. Consequently the names *H. cordifolius* Miq. and *H. lupulus* L. var. *cordifolius* Maxim. are placed in synonymy with *H. lupulus* L.

Morphology

Until recently only brief accounts of hop morphology had been published despite very extensive studies conducted upon certain parts of the plant. Within the last two years, however, this situation has radically changed. Ehara (1955) has made a comparative study of *H. japonicus* Sieb. & Zucc. and *H. lupulus* L., including anatomical observations as well as descriptive comparisons starting from the seedling stage. Hamaguchi (1955) published an even more extensive work on *H. lupulus* L. including developmental analysis of the vegetative and flowering shoot. As a consequence of these publications, a detailed account of the morphology of the hop plant will not be presented here, though a description of the inflorescence of the female plant is required for the discussion which follows. Unless otherwise indicated, all observations apply to *H. lupulus* L.

The small pistillate flowers, each consisting of a cup-like perianth and a single pistil with two elongate stigmas, are borne in the axils of bracts and bracteoles upon a condensed axis, forming the cone. Multicellular glands, containing lupulin, are found in great number upon the bracts and bracteoles.

The cone itself is a greatly condensed inflorescence, readily differentiable into nodes and internodes. At each node are normally found four flowers. This node is really a complex structure best understood from fig. 1 (modified after Hamaguchi, 1955, p. 94) in which three are diagrammed. The internodes a^1 and a^2 are reduced to the point where they are barely visible, thus condensing two nodes of these secondary axes back upon each node of the primary axis.

The nodal cluster has been interpreted as cymose, with the median flowers abortive (fig. 2). When all bracts and bracteoles are removed, the cone appears in side view as shown in fig. 3A. Each nodal cluster then appears to be subtended by a single bract scar. When turned through 90°, however, it is seen that two

[16] In Franchet & Savatier's Enum. Pl. Jap. 2:489. 1879.
[17] Ann. Mus. Bot. Lugd. Bat. 2:133. 1865.
[18] Jour. Bot. (Brit. & For.) 20:293–294. 1882.

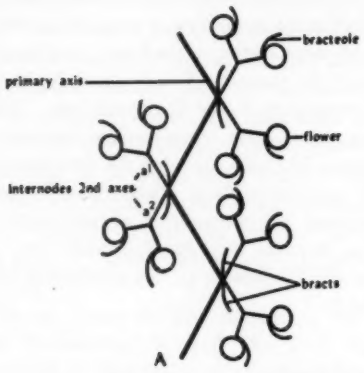

Fig. 1. Diagram of a hop cone showing three nodes. Internodes of secondary axis are much enlarged.

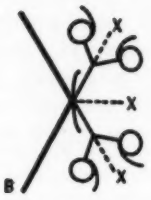

Fig. 2. A cluster of flowers at a single node of cone. Abortive flowers indicated by X.

scars occur at the base of each cluster of four flowers (fig. 3B). Rendle[19] has interpreted these as stipules of a former bract. Though the two scars are not usually inserted at the same level, one appearing slightly above and overlapping the other, the infrequent cone with well-developed foliage leaves confirms Rendle's interpretation. In such cases the petiole is found directly between the two scars, which are at the same level (fig. 3C). The slight displacement found in the normal cone must be attributed to a secondary effect of growth. Moreover, these stipular bracts (which are so widely known in the hop literature simply as bracts that they will be so called henceforth) show a vein pattern similar to that of the stipules throughout the vegetative parts of the plant, while being very different from that of the bracteoles.

MATERIAL

Much of the analysis of hops throughout this study has been based upon cones. They contain many diagnostic characters and are readily obtainable from many parts of the world. Some of the cones used for analyses were small samples taken from the pressed bales which are submitted to brewers for their evaluation of the crop. Though the cone material itself is not inferior to field collections, it is of course not possible to determine the number of plants represented in any such sample. The elaborate method of machine picking so thoroughly mixes up cone material that as an approximation each cone may be considered to represent a different plant. In addition to the brewers' samples, cones and leaf collections have been made in the field. With these, though each cone is selected from a different plant, the number of clones represented may be small.

[19] Classif. Fl. Pl. 2:56–58. 1952.

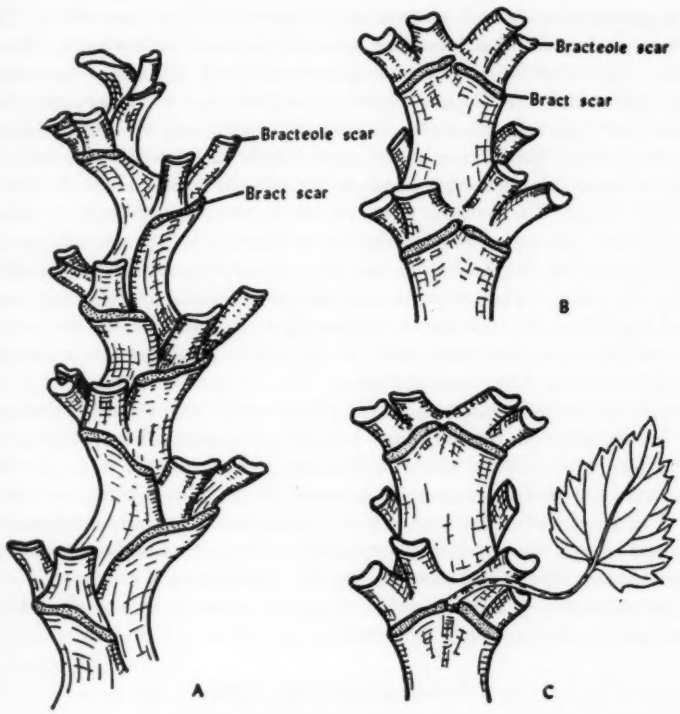

Fig. 3. Hop cone axis with bracts and bracteoles removed: A, resting on flat surface; B and C, turned on edge; C, abnormal cone bearing foliage leaf.

Some knowledge of field practices is imperative for an understanding of the field samples. Ideally, every hop field of the same variety belongs to the same clone. Vegetative reproduction, by cuttings, is the only method used commercially. Each spring, or for the sake of economy every several years, soil is dug back from the hop hill and all but a few of the young shoots are cut off. The cut shoots are then used to replant old hills, or for new plantings. It is a standard procedure for farmers to sell excess hop roots to neighboring farmers, or at the present time, in the large organizations of growers, to ship roots from state to state. Only rarely, when new fields are being established, will such additions be kept separate. More generally new plantings are intermixed with old. This, by itself, would not offer complications if each variety remained true to type. However, not only have some new varieties been attributed to bud sports, but innumerable worthless rogues occur each year. The superintendent of one farm in California reported he was removing almost 20 per cent of the hills because they

were off type. This was after many years without roguing, but several farmers have suggested that about 5 per cent of the plants each year are rogues. To my knowledge, no research has been done upon the source of such rogues. They may represent vegetative mutations, seedlings, or carelessly introduced contaminants.

The tale told by an Oregon farmer (though it may be an unusual case and somewhat exaggerated) illustrates how contaminants may be introduced during replanting fields. He had purchased roots which he believed to be of a single variety of hop. After planting them on his own farm two-thirds of them grew into willow trees! The sequence of events which led to this can easily be followed. In many areas, the spring root cutting is not done under the surveillance of the superintendent, but the field is let out to a cutter who receives as pay the root cuttings he makes. The temptation to add to the yield by collecting roots of escaped hops from the roadsides is occasionally too great. To the contamination from such weed hops had been added the frequently present willow whose shoots are readily confused with those of hops.

Besides the over-all sampling problem which results from the field heterogeneity is the heterogeneity of the individual hop hill. Almost without exception more than one root is planted per hill; most frequently the number is three. In making the collections of leaves and cones I attempted always to take both from the same vine. Usually the effort was successful. However, since four (or more) vines are trained to each wire, and these vines may originate from different root stocks, it was necessary to trace the cone-bearing side branches back to the main vine at the level (5 or 6 feet above ground) at which leaves had been selected. This always introduced opportunity for error.

Varietal Identification

Before turning to the morphological characters which have been used here, some previous efforts to describe varieties on structural characteristics will be considered. In the description of new varieties, it has been a standard practice to make use of cone shape, size, and coloration. Such descriptions are of obvious use to the grower, at least in so far as they are not too generalized. Unfortunately, exactness is not easily attained. Moreover, cone shape and size are greatly influenced by pollination. For instance, a variety such as LATE CLUSTERS, which produces long cones with prominent dark green streaks (the bracts) alternating with light green streaks (the bracteoles) when unpollinated, regularly has nearly spherical cones, without streaks, after pollination. Although this type of varietal description is useful to growers familiar with these changes, it is not suitable for describing pressed material, nor is it of great value to the botanist or geneticist. It is only when more definitive characters are used that it will be possible to trace the inheritance patterns in hops.

Beyond studying the varietal descriptions, many efforts have been made to study other morphological features of hops. Only a few need be mentioned here. Wormald (1915) undertook an extensive examination of male hops. Leaf color,

texture, lobing, dimension of lobes, gland number and distribution were scored. Salmon and Wormald (1921) studied time of flowering, color of stem, relative number of glands on the leaves, and on the cone; size, shape, aroma, and color of the cone axis. Schmidt (1918) investigated the possibility of characterizing clones by the number of marginal teeth on the leaves. This investigation, carried out over a number of years, provided valuable information on the change in leaf shape which takes place as a plant becomes established. More recently, Meneret et al. (1954) have reported on the use of the length-width ratios of bracts as a means for varietal identification.

In the present study six characters have been chosen for scoring. They represent various modifications of the characters previously used. Even more important is the semi-graphic method of expressing the results (Anderson, 1949). By this means it is possible to identify a hop sample by plotting it out and comparing it with previous plottings of known varieties. The advantage is not only in its usefulness in identifying varieties, but also in that genetical relationships are suggested when suitable botanical characters have been selected for scoring. Identification of hop varieties is not the primary concern of this paper. Rather attention is being focused upon the morphological complexes within *H. lupulus*. Evidence suggests that these complexes, which are based entirely upon structural features, correspond to certain chemical and perhaps cytological groupings within the species. If additional research confirms this, such morphological features as are used here will have an increased value in hop breeding. At the same time it will provide an interesting example of the use of chemical, morphological, and cytological evidence for the establishment of taxa below the level of species, where morphological evidence is not adequate by itself.

The following six characters have been scored and the results expressed in pictorialized scatter diagrams: On the leaf: (1) dentation number, (2) pubescence type. On the cone axis: (3) condensation; (4) angularity; (5) bract scar type. On the bract: (6) number of main veins extending into the terminal third.

LEAF:

(1) *Dentation.*—The leaf shape, and consequently the dentation number, is exceedingly variable upon each hop plant. To attempt to describe plants upon the basis of a few randomly selected leaves would be impossible; merely increasing the number of leaves sampled has not proved very satisfactory. Leaves found at the lowermost nodes are distinctly different from those at higher nodes and in the inflorescence. The leaves of the secondary and tertiary axes differ from those of the primary. Despite this great variation, truly homologous leaves may be obtained by making the selection from a main vine (one of the vines trained up from the hill) of a mature plant. In this way, the phenotypic variability can be reduced to measurable proportions. The leaves in all field collections have been taken from the main vine, at a height of about five or six feet. The dentation count was made on the median lobe of the leaf in the following manner: From the number of all

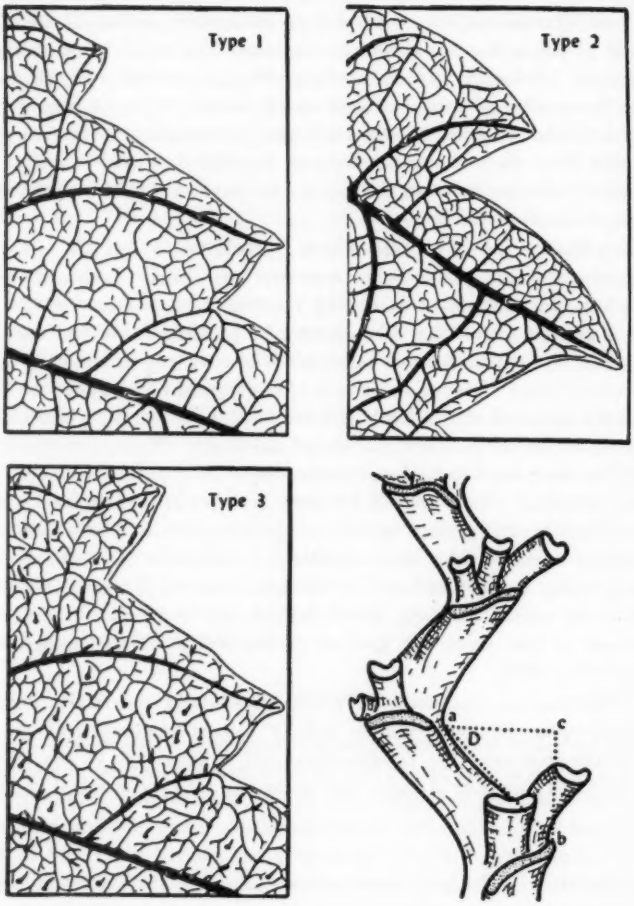

Fig. 4. Under surface of hop leaf drawn at margin, showing three different pubescence patterns. Lower right, showing method of measuring angularity.

dentations counted, was subtracted the number which were not provided with a distinct vein visible to the unaided eye, the result giving the "major dentations". The number of minor dentations was also recorded in each case, but was so variable within every variety that it did not contribute to their identification and has been eliminated. In addition, the number of dentations within 5 cm. from a point on the edge of the lobe to the last dentation at the lobe apex was counted.

Since Schmidt's work (1918) had shown that dentation number steadily in-

creased during the first three years that a plant is becoming established, collections were made only from plants four years or more old, unless otherwise indicated.

(2) *Pubescence.*—The number of hairs per unit area upon the under side of the leaf undergoes tremendous variation, and is not by itself a satisfactory character. Of greater importance than the number is the pattern of their distribution. Upon all hop leaves, hairs are found on large veins. Type 1 was made up of leaves with hairs on major veins only; type 2 with hairs upon these and upon secondary veins as well; type 3 was characterized by the presence of hairs upon all veins, down to those of the smallest, and between veins on the vein islands. These types are shown in fig. 4. In most cases, type 3 possessed the most hairs in an absolute sense, but when the leaves approached the glabrous condition, hairs were not confined to large veins, as in the nearly glabrous leaves of type 1. With but few exceptions known clones remain constant as to type.

CONE:

(3) *Condensation of the axis.*—Using a dissecting scope, the length to the nearest mm. was measured between five bract scars. These were taken at the base of the cone, or at least never including the two uppermost nodes.

It is to be expected that the greatest disturbing influence upon this and the following character is pollination. Since pollination is known to produce profound changes in the cone axis, only unpollinated (seedless) cones are compared, unless otherwise indicated.

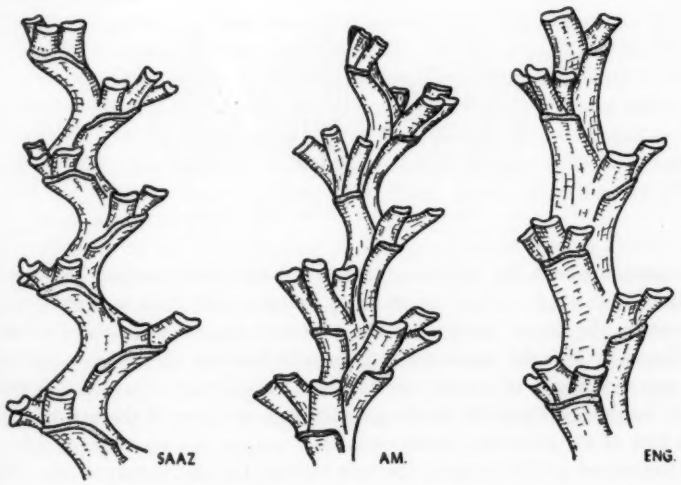

Fig. 5. Cone axis of three different varieties: SAAZ, Czechoslovakia; AM, LATE CLUSTERS; ENG, FUGGLES.

(4) *Angularity of the axis.*—The angularity of the axis was measured with the use of an eye-piece micrometer and dissecting scope. A line *ab* (fig. 4) was drawn with the micrometer parallel to the axis, and then lines *ac* and *bc* were measured; from the right-angle triangle so constructed, angle *D* was obtained. This angle was in turn doubled, thus giving an approximation of the angle naturally formed.

(5) *Bract scar.*—The scar left by removal of the bract, when seen in side view, is classified as either elongated (stretching nearly between nodes of the axis, fig. 5 SAAZ) or abbreviated (confined to the area immediately below the subtended fruits, fig. 5 ENG.).

The type of bract scar served to make a major division between varieties. The scar is definitely independent of the degree of condensation or angularity of the axis as is shown by the retention of form without regard to the changes produced by pollination.

BRACT:

(6) *Vein number.*—Brewmasters have long realized that different varieties have different-shaped bracts. Such differences may be of considerable value though the variation within a cone, from base to tip, is great. Meneret et al. (1954) have been determining length-width ratios over a period of years. Though their report is optimistic, they concluded that this measure was "not completely definitive and should be considered along with other characteristics in identifying the type." Here, the same problem was approached in another fashion: the number of major

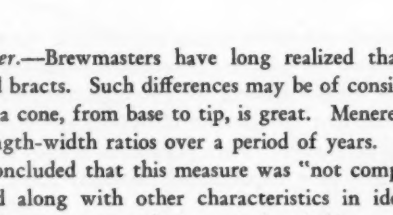

Fig. 6. Three principal bract types.

veins extending into the terminal third of a bract was recorded. This is itself correlated with shape, a low count being found on the long acuminate bract, a high one on the obtuse bract. For the present it appears to be more satisfactory than shape, at least for establishing differences between complexes. However, a more specific measure is necessary if individual varieties are to be differentiated. In order to establish uniformity for the measurement used, one of the first three bracts at the base of the cone was chosen each time.

When scored in this manner, the vein number for any variety is not constant. The range varies with the variety, but even with this variation, the populations fall into groups 7–8, 9, 10 or more. Fig. 6 shows a bract of each type.

Varietal Stability

Among the most discussed, but least exactingly studied, characteristics of hops, is their reputed ability to adapt to each new environment and assume the qualities attributed to that particular region. Such views are still widely found among growers. One of the popularly held examples of this "adaptation" is based on the effect of pollination upon cone shape and color as mentioned above. LATE CLUSTERS produces long cones with dark green and light green stripes when grown in California, Washington, and Idaho. Those in Oregon have more nearly spherical cones without striping. The essential difference between these types is not in the area in which they are grown, but in the presence or absence of seeds. The Oregon area hops, which are always seeded, have a characteristic cone, as do the uniformly seedless California forms.

In the selection of the foregoing tools of analysis, a strong emphasis was placed upon the stability within a clone as a measure of reliability. That fact at once prejudices their use in the evaluation of the uniformity or variability as it exists within each variety over time and space. A comparison of LATE CLUSTERS from California, Washington, and Idaho, for the year 1955 (figs. 7 and 8) shows how little the difference is, in these morphological characteristics at least, within that geographical range. The variation is not significantly greater than the individual plant variation shown in fig. 9, in which the leaf and cone measurements have been arbitrarily combined.

Another comparison is based upon leaf scores only. Fig. 10 shows leaf lobe number and dentation scores for LATE CLUSTERS. For the populations studied, the leaf lobe number was greater in Idaho (median 7) than in California or Washington (both with median 5). The dentation number is also greater in Idaho (42) than California (38) or Washington (36). That this may be attributed to larger leaves in the well-irrigated fields of Idaho is indicated by the dentation count per 5 cm. of leaf margins, both California and Idaho having a median of 12 and Washington a median of 11.

The constancy in the morphological characters measured here in different geographical areas speaks well for varietal consistency. The number of morphological characters which may undergo some change of course is not known, but they are certainly not of enough magnitude to warrant a fear of varietal instability. It must be recognized that genetically based characters may be such that they will remain virtually unchanged over the area within which the plants may grow, or they may be capable of a fluctuating expression under changing conditions. In the latter case, they are no less genetic.

EXPLANATION OF SYMBOLS USED IN SCATTER DIAGRAMS
(FIGS. 7–9, 12–14)

Number of main veins at tip of lower sterile bract:

7-8
9
10-11

Pubescence:

Hairs on main vein only
Hairs on main and minor veins
Hairs on and between veins

Number of teeth on median lobe of leaf:

20-26
27-33
34-+

Bract scar:

Elongated
Abbreviated

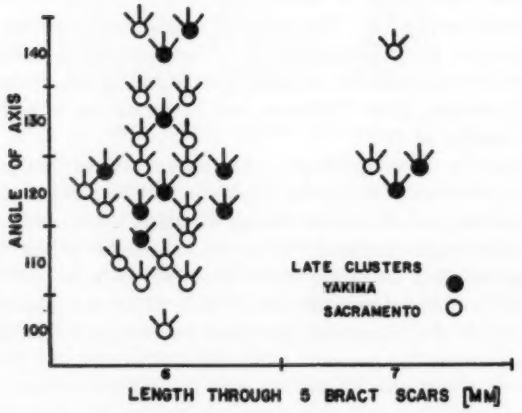

Fig. 7. Pictorialized scatter diagram of LATE CLUSTERS from Washington and California.

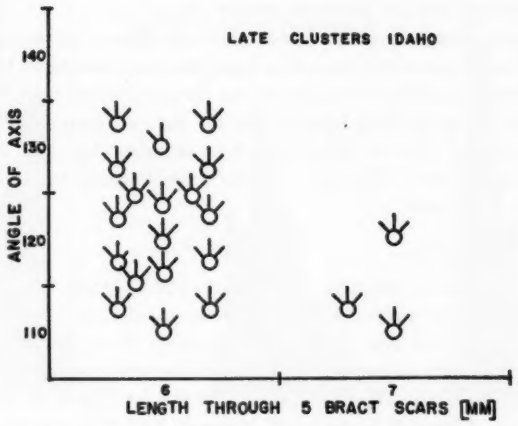

Fig. 8. Pictorialized scatter diagram of LATE CLUSTERS from Idaho.

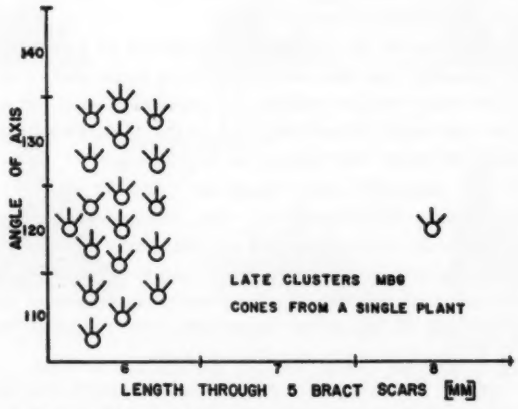

Fig. 9. Pictorialized scatter diagram of LATE CLUSTERS, leaves and cone taken from a single plant.

DISTRIBUTION OF VARIETIES WITHIN MORPHOLOGICAL COMPLEXES

The lobe and dentation scores for LATE CLUSTERS and FUGGLES, BREWER'S GOLD, BACKA, and HALLERTAU are presented in figs. 10 and 11.

Pictorialized scatter diagrams based upon populations of FUGGLES, BREWER'S GOLD, BACKA, and HALLERTAU hops have been presented elsewhere (Davis, 1956). It is sufficient here to consider composite scatter diagrams which have been plotted for these and other varieties using mean values for the axis measurements and median arm scores. One of these is based upon field samples (fig. 12) and is therefore scored for all characters. The other is based upon brewing samples (fig. 13) and does not show leaf scores.

Interpretation of results.—

Though the leaves of FUGGLES, BACKA, and LATE CLUSTERS all have median lobe numbers of 5, there are marked differences in the populations. FUGGLES and BACKA hops, not known to have any American relationship, have virtually no leaves with more than 5 lobes, and are outstanding in their uniformity. Seven-lobed leaves are frequent on plants of the American LATE CLUSTERS, and up to 10 lobes may occur. BREWER'S GOLD, an English variety with a female "wild" parent from Canada, has even a larger proportion of 7-lobed leaves, though the maximum is again 10. While large collections will show these differences strikingly, and it seems reasonable to attribute differences in potentiality to these varieties, individual plants can not be identified by this leaf character because of the great overlap between varieties.

In total dentation number, the European varieties are low, and distinctly separate from the American LATE CLUSTERS.

The scatter diagrams of the individual populations of LATE CLUSTERS (figs. 7 and 8) are more variable than the collection from a single plant (fig. 9). Though this suggests that every member within the population may not be of the same clonal origin, the variation is minor compared to that occurring in the Oregon field (fig. 14) in which off-types were known to be growing.

A study of the composite scatter diagrams (figs. 12 and 13) suggests that cultivated hops fall into three complexes: One, with a much-condensed very angular axis; a second with an elongate, straight axis; and a third, somewhat between the two in axis characters, but extreme in leaf and bract characters. Considering the history and region of cultivation of the varieties composing these complexes, the complexes are seen to consist of hops from (1) Germany, Czechoslovakia, Yugoslavia, (2) England, and (3) the United States.

Bringing together the cone axis, pubescence, dentation and lobing measurements, the three morphological complexes may be described as follows:

(1) *Continental complex:* Cones with condensed axis, markedly zig-zag; bract with 8 veins extending into the terminal third; elongated bract scar, reaching between nodes of axis; leaves with low number of dentations and lobes. On the undersurface of the leaf, hairs on major and minor veins but not between veins

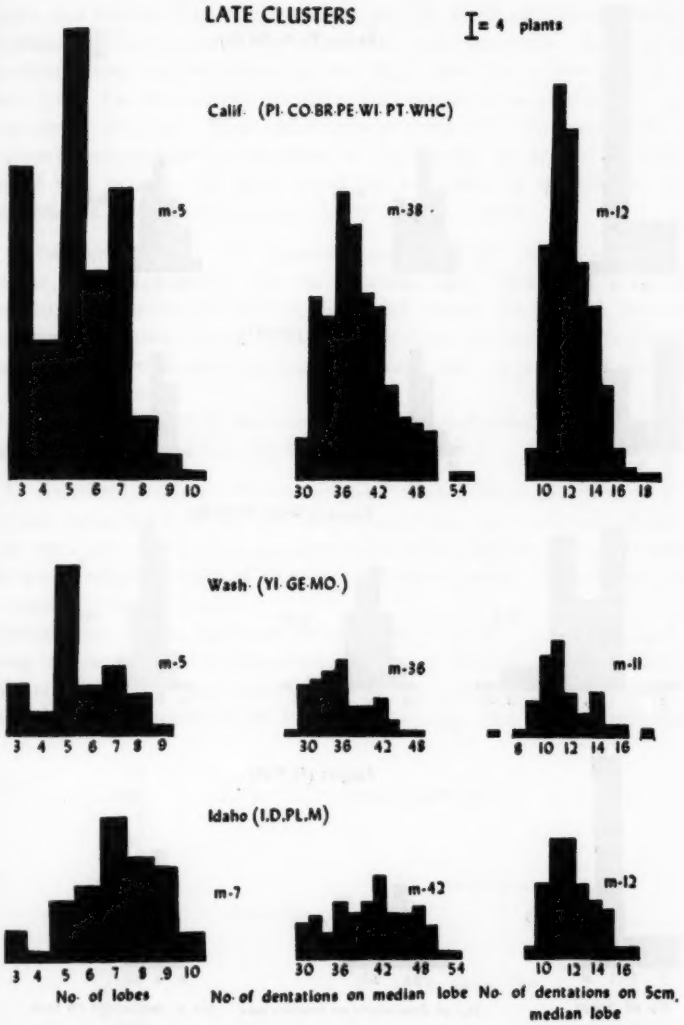

Fig. 10. Scores of leaf lobe and dentation number for LATE CLUSTERS from California, Washington, and Idaho.

(type 2). Though only a single variety (HALLERTAU) of this complex has been studied extensively for pubescence, the uniformity in cone structure throughout the group suggests that the leaves may be very similar also. This is given some additional support from the types of pubescence found on European herbarium

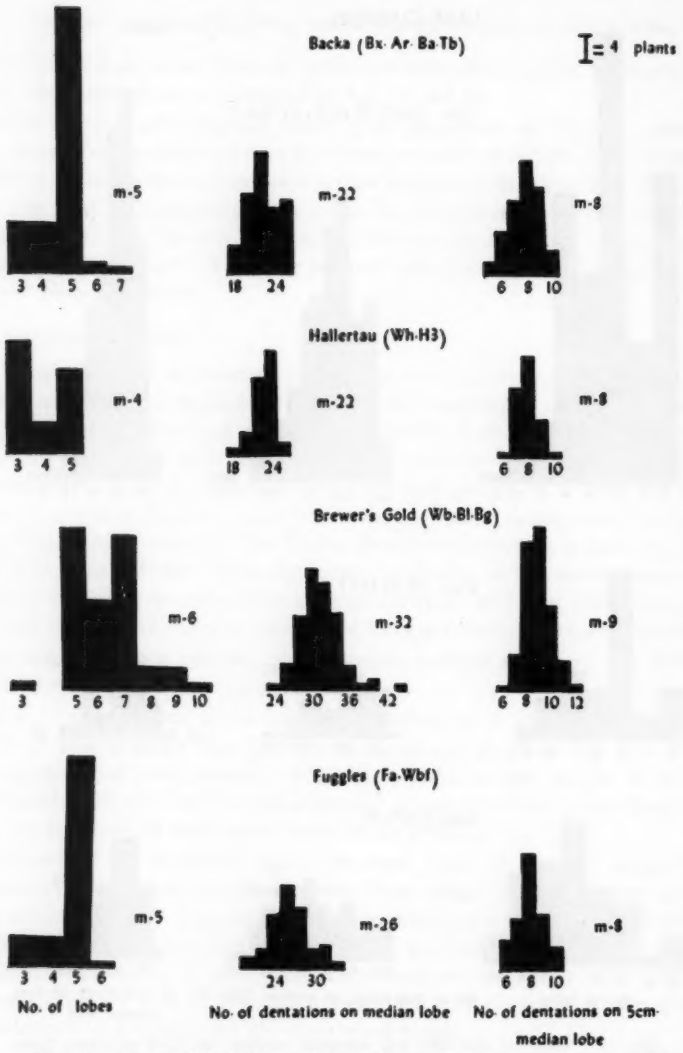

Fig. 11. Scores of leaf lobe and dentation number for BACKA, HALLERTAU, BREWER'S GOLD, and FUGGLES.

specimens of reputedly wild growing hops. A representative cone axis is shown in fig. 5 (SAAZ).

At the present, within the complex of continental hops it is possible to establish a gradation, starting with HALLERTAU and SAAZ, and running through TETTNANG

to BACKA and STYRIAN hops. It is not yet possible to identify every variety positively due to the limitations of the material available for study. Brewing samples of continental hops may not always be of a single type, but of two or more closely related types. The replacement of cultivated varieties in the field is often gradual and not always complete. When closely related types are in the same sample, whatever variation occurs must be considered as representing the natural limits of variability of that variety. As more characters are added to the complex, it will become possible to separate out even closely related varieties.

(2) *English complex:* Axis expanded, nearly straight; bracts with 7 or 8, or sometimes 9 veins, extending into the terminal third; abbreviated bract scar restricted to area immediately beneath subtended flowers; leaves with low number of dentations and lobes, though in some greater than type one. Nearly glabrous on the lower surface with hairs confined to main veins (type 1). Representative cone axis fig. 5 (ENG.).

Additional study will be necessary to determine if other varieties grown and developed in England fall into the English complex.

(3) *American complex:* Cones expanded, slightly zig-zag; bracts with 10 or more veins extending into the tip; abbreviated bract scar indistinguishable from that of type 2; leaves with high number of dentations and lobes when mature, hairs on the lower surface on veins of all sizes, and between veins. A representative cone axis is shown in fig. 5 (AM).

Though considerable care must be exercised in making comparisons, it is interesting to note the general correspondence between these morphological complexes and the classification of hop varieties according to the cohumulone content of the alpha-acid fraction presented by Rigby (1956). In that classification Group I

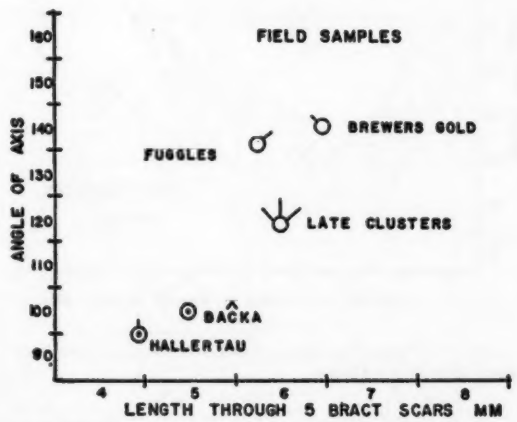

Fig. 12. Pictorialized scatter diagram of varieties indicated based upon field samples. (For explanations of symbols see p. 284).

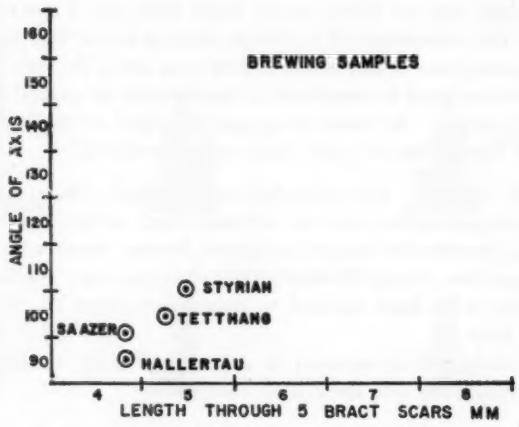

Fig. 13. Pictorialized scatter diagram of varieties indicated based upon brewing samples.

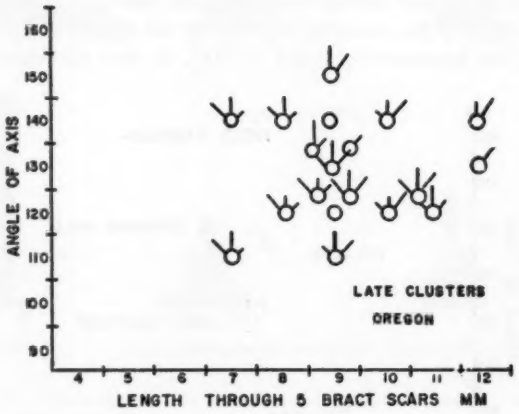

Fig. 14. Pictorialized scatter diagram of LATE CLUSTERS from poorly kept field in Oregon.

consisted of SAAZ, Bavarian and British Columbia HALLERTAU, Yugoslavian and Washington BACKA, and TETTNANG. This corresponds to complex 1, with the exception of the variety STYRIAN, which was placed as the extreme in that complex. In the classification based upon the cohumulone content, STYRIAN falls into Group II with Oregon FUGGLES and other varieties not considered here. Rigby's Group III contains among others, BREWER'S GOLD and Washington SEEDLESS (a trade name usually designating LATE CLUSTERS). Group IV consists of California and Yakima SEEDLESS (LATE CLUSTERS?). Until the same samples are examined for chemical and morphological features it will not be possible to determine the degree of agreement between the two systems, particularly for the American hops where different trade names may be used for the same variety, and a single commercial sample may contain several botanical varieties.

THE AMERICAN WILD HOP

Wormald's (1915) careful study of Oregon male hops led him to believe that the Oregon hop was very different from the hops of England. Consequently, Salmon and Wormald (1921) suggested the retention of the separate species *H. americanus* Nutt. Their conclusions did not receive general acceptance for these reasons: (1) The number of plants involved in the study was small. (2) It was not possible for them to make extensive analysis of either the cultivated or wild-growing American hops. (3) The various differences which they found were not sharp enough to separate the English and American hop, and the comparison was not carried to hops cultivated in other countries.

It now appears, however, that there are differences between the American culti-

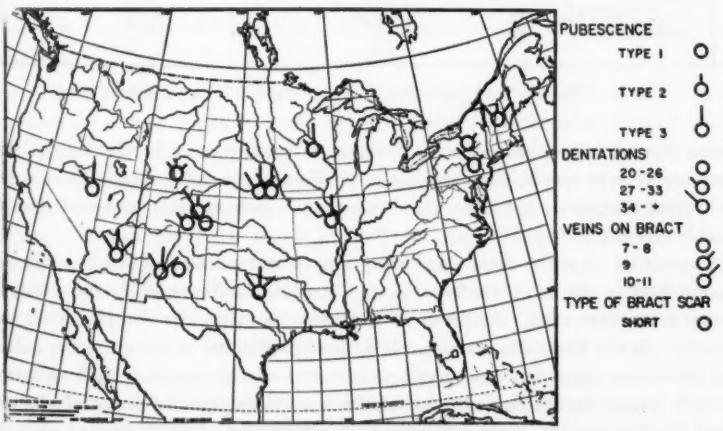

Fig. 15. Distribution of wild hop types in the United States. Scored in the same manner as the cultivated hops, but based upon herbarium specimens of wild-growing hops.

vated varieties LATE CLUSTERS and other varieties cultivated throughout the world which can also be found between American wild hops and the wild hops of Europe.

In the present study, characters generally different from those used by Wormald (1915) suggest a unique American cultivated hop. In the analysis of presumably wild hops represented by herbarium material it has not always been possible to make the same sort of measurements of these characters as used in the study of field collections of cultivated plants. All too often, herbarium material is incomplete and does not permit examination of both cones and foliage. For those specimens where complete measurements were possible, the results for the United States are shown in fig. 15, using the same symbols as in the pictorialized scatter diagrams. Fig. 16 shows the distribution of pubescence types in the United States.

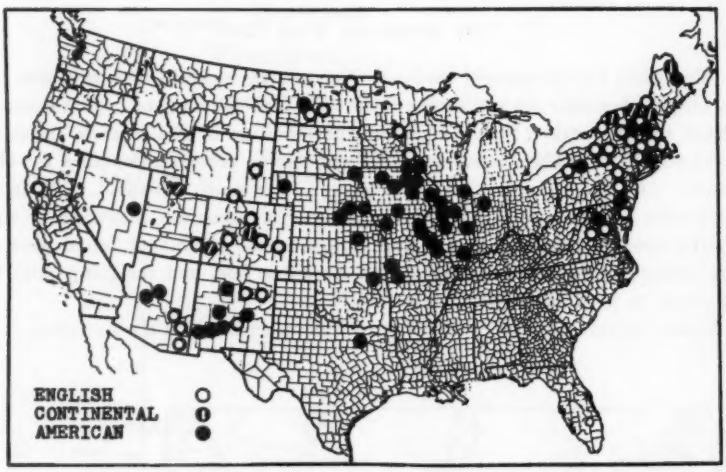

Fig. 16. Distribution of the three pubescent types of hops in the United States.

I have observed the pubescence type three, so predominant in the United States elsewhere only in specimens from Japan, possibly as a result of introduction from the United States. It is known that American hops have been imported into that country (Ehara, 1955).

Considered together, these maps bring out several interesting points. The midwestern hop is the most uniform in the country, and resembles the cultivated variety LATE CLUSTERS. Forms from both the East and the Southwest are more variable. In the East, this condition is at least partly due to escapes from cultivation, since the region was once an important area of cultivation. Such escapes are certainly much less frequent in the Southwest. Very possibly many of the types found in that area are truly indigenous, in which case LATE CLUSTERS represents only a portion of the variability of the American wild hop.

To the morphological differences between the American and European hop can be added cytological differences. Ono (1955) found the Sinoto type sex chromosome complex in Japanese and American wild hops, but not in European wild ones. An examination of a few specimens from plants for which he had determined the chromosome type showed a correlation of the American morphological type and the Sinoto type sex chromosomes. More extensive cytological investigation is required to confirm this but it lends support to the separateness of the American hop. However, the differences between the American and European wild hop, though distinct, are so slight that it would not seem advisable to establish separate names. Furthermore, until the limits of variability within the American segregate are more clearly understood, as well as the relation of the American and the Japanese plant, it is preferable to use the name *Humulus lupulus* for all wild perennial hops.

Summary

1. The nomenclatural problem in the genus *Humulus* has been reviewed. Particular attention has been devoted to efforts to establish an American taxon. It has been shown that the various characters previously did not conclusively establish a native American hop distinct from the hop of Europe.

2. Due to the ease with which the perennial hop escapes from cultivation, it is suggested that the wild and cultivated plant must be studied simultaneously.

3. A method for measuring hop variation, based upon leaves and cones, is described and applied to collections of cultivated plants, brewing samples, and herbarium material. The measured characters are shown to be stable for each variety over a wide geographical range. The cultivated hops are found to fall into three morphological complexes. One is represented by English varieties, another by German-Czechoslovakian varieties, and the third by the American variety LATE CLUSTERS.

4. An examination of the presumably wild hops in the United States shows that there are characters in common between them (and the wild hops of Japan) and the cultivated variety LATE CLUSTERS, which are unknown in European hops. This is in apparent agreement with Ono's finding of the Sinoto type sex chromosome complex in American and Japanese wild hops, but not among European ones. However, though the wild hop is uniform in the midwestern area of Illinois, Missouri, and Iowa, it is very variable in the Southwest, where it is known to be indigenous. It is at present not possible to set the limits on the variation in the truly native American hop so as to exclude all European ones. Moreover, the differences between hops from Europe and the United States are such that both vegetative and fruiting material (so often absent on herbarium specimens) are essential for a proper identification. Consequently, it is recommended that the name *Humulus lupulus* L. be applied to all perennial hops, at least until such time as the native American hop is more thoroughly understood.

Acknowledgment.—Appreciation is expressed to the Brewing Industries Research Institute and the Fixed Committee on Hop Studies for their assistance and financial support in this investigation, and to the curators of the herbaria of the Bailey Hortorium, of Harvard University, and of the Missouri Botanical Garden, who have lent specimens for this study.

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ANDROCALYMMA, A NEW GENUS OF THE TRIBE CASSIEAE (CAESALPINIACEAE)

JOHN D. DWYER*

Androcalymma Dwyer, gen. nov.

Arbores. Folia imparipinnata foliolis petiolulatis alternis vel oppositis tenuiter coriaceis costa supra immersa. Flores cymulis in paniculam terminalem dispositi. Sepala 5 imbricata; petala 5 imbricata unguiculata intus carinata. Stamina 4 libera aequalia partim circum pistillum disposita antheris biporosis rectis vel deflexis subversatilibus connectivo gracillimo. Ovarium subsessile complanatum ovulis paucis.

Trees. Leaves imparipinnate, the leaflets alternate or opposite. Flowers in cymules in a terminal panicle. Stamens 4, equal, the anthers erect or deflexed, subversatile, the connective slender. Pistil subsessile with few ovules.

Type Species: *Androcalymma glabrifolium* Dwyer.

Androcalymma glabrifolium Dwyer, sp. nov.

Arbores circ. 30 m. altae. Ramuli ultime valde lenticellati teretes glabri. Petioli 3–6 cm. longi, 0.1–0.5 cm. lati, plani glabri; stipulae non visae. Folia aequilateralia ovato-elliptica, 4.5–10 cm. longa, 2.5–5.5 cm. lata, plus minusve apice acuta basi obtusa tenuiter coriacea supra nitidula laevia glabra costa infra immersa prominente basi circ. 1.5 mm. lata, venis principalibus secundariis 8–12 prominulis arcuatis venulis laxis reticulatis marginibus parum callosis; petioluli 5–7 mm. longi graciles glabri. Flores in cymulis paucifloris dispositi, rhachidibus evidenter quam superioribus foliis brevioribus gracilibus basi ad 1.5 mm. latis basi articulatis; bracteae bracteolae caducae cicatricibus prominentibus. Sepala 5 aestivatione valde imbricata inaequalia oblonga vel ovato-oblonga circ. 3 mm. longa 1.8–2 mm. lata apice obtusa extus pubescentia ciliis mediis saepe densius dispositis intus glabra carnosa marginibus sparse ciliolatis; petala 5 subaequalia aestivatione valde imbricata oblonga 4–6.5 mm. longa 1.7–2 mm. lata apice obtusa basi unguiculata, unguibus ad 0.5 mm. longis, extus pubescentia intus glabra et evidenter carinata; stamina 4 filamentis subcrassis saepe subclavatis rectis, 2–3 mm. longis circ. 0.25 mm. in medio latis glabris mox deciduis; antherae ovato-subrotundae circ. 0.6 mm. longae vix apice biporosae subrectae vel deflexae subversatiles, connectivo circ. 0.2 mm. longo paullum thecis obscurato, 4-locellatae at 2 loculis; ovarium vix stipitatum vel subsessile complanatum oblongum circ. 2 mm. longum leviter omnino pubescens 2–3-ovulatum stylo brevissimo. Fructus non visi.

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*St. Louis University and Missouri Botanical Garden, St. Louis, Mo.

Issued January 29, 1958.

Type Collection: *Krukoff 9005*, Municipality São Paulo de Olivença; basin of Creek Belém, terra firma, high land, Amazonas, Brazil (HOLOTYPE MO, isotype NY).

The fancied resemblance of the anthers when deflexed to a drawn cowl suggested the name, *Androcalymma*.[1] The pinnately compound leaves and the porocidally dehiscent anthers readily place it in the tribe Cassieae. Several floral characters point to its relationship with *Dicorynia* Benth. and *Martiusia* Benth. of the same tribe: the imbricate sepals and petals borne on a fleshy receptacle, the lack of an obvious hypanthium, the few stamens only partially surrounding the ovary, and the very shortly stipitate ovary. The flowers disposed in numerous few-flowered cymules and the imparipinnate leaves with alternate or opposite leaflets likewise suggest this relationship. Both *Martiusia* and *Dicorynia* are well distributed in the Amazon Basin as well as in the Guianas.

Several features of the androecium as well as the very short style of the pistil serve to distinguish *Androcalymma* from its allies. The filaments of the new genus are much more elongate than those of *Martiusia* and obviously less crassate than those of *Dicorynia*. The latter genus has only two stamens. The anthers of *Martiusia* are subulate and acuminate. *Dicorynia*, with unequal filaments, has larger anthers which are 4- or 8-locellate. The presence of 8 locelli in one or in both of the anthers distinguishes *Dicorynia* from all other genera of the Caesalpiniaceae.

Worthy of special note is the slender attenuate filament tip attached to the anther of *Androcalymma*. This usually lies well hidden between the locules which are free at the base. It is difficult to trace the filament tip to the point of insertion on the connective, the base of the latter being well above the base of the locules. The subversatile condition of the anthers is apparently found elsewhere in the tribe Cassieae only in occasional species of *Cassia*.

Krukoff, the collector of the type material, notes that the tree is 100 feet high, and that the trunk measures 18 inches in diameter.

I wish to acknowledge the help of several specialists who made notations on the herbarium sheets and carried on correspondence concerning the new genus. These include: A. Ducke, R. Schery, J. Monachino, N. Y. Sandwith, and R. Cowan. Special thanks are due the last three.

[1] ἀνήρ (man); καλύμμα (cowl).

Fig. 1. *Androcalymma glabrifolium* Dwyer

A REVISION OF THE GENUS *STYLOSANTHES**

ROBERT H. MOHLENBROCK**

History of the Genus

The genus *Stylosanthes* was established in 1788 by O. Swartz[1] with two species, *S. procumbens* (= *S. hamata* (L.) Taub.) and *S. viscosa*. Previous to the founding of the genus, most present-day species of *Stylosanthes* had been referred to other genera. Linnaeus[2] in 1753 had described *Trifolium biflorum* (= *S. biflora* (L.) BSP.) and in 1759[3] *Hedysarum hamatum* β (= *S. viscosa* Sw.); in 1775 Aublet[4] had named *Trifolium guinanense* (= *S. guyanensis* (Aubl.) Sw.).

Preceding the advent of the binomial system, a few polynomials had been applied to modern species of *Stylosanthes*. Apparently the first mention of a species now known to belong to the genus was in 1696 when Sir Hans Sloane[5] listed *Anonis non spinosa, minor, glabra, procumbens, flore lutea* as occurring in Jamaica. This is *S. hamata* (L.) Taub. In 1737 Burmann[6] recorded *Trifolium procumbens zeylanicum hirsutum* (= *S. fruticosa* (Retz.) Mohlenbrock).

Willdenow, in the fourth edition of 'Species Plantarum',[7] listed five species of *Stylosanthes*. G. Don[8] in 1832 listed thirteen species. Of these, however, only seven have proved to be distinct, and three of these were recorded without usage of the earliest epithet applicable.

The first study of *Stylosanthes* was a synopsis by Vogel[9] in 1838. He divided the genus into two sections, EUSTYLOSANTHES and STYPOSANTHES, based on the absence or presence, respectively, of an axis rudiment (an aborted secondary axis associated with each flower). An unfortunate situation has arisen, however, since Vogel designated *S. procumbens* Sw. (= *S. hamata* (L.) Taub.) of § STYPOSANTHES to be the type species. According to present nomenclatorial rules, the section or subgenus including the type species must repeat the generic name, hence Vogel's § STYPOSANTHES must be changed to § STYLOSANTHES; his § EUSTYLOSANTHES here is renamed § ASTYPOSANTHES. In his section including species without axis rudiments, Vogel recorded eight species, three of them new, while in the other section, seven species are listed including four new ones. All seven of Vogel's new

[1] Swartz, O. Prod. Veg. Ind. Occ. 108. 1788.
[2] Linnaeus, C. Sp. Pl. 773. 1753.
[3] Linnaeus, C. Syst. Nat. 10:1170. 1759.
[4] Aublet, F. Pl. Guian. 776. 1775.
[5] Sloane, H. Cat. Pl. 1696.
[6] Burmann, J. Thes. Zeyl. 1737.
[7] Willdenow, C. Sp. Pl. 3:1166. 1800.
[8] Don, G. Gen. Syst. 2:281. 1832.
[9] Vogel, in Linnaea 12: 68. 1838.

* An investigation carried out in the graduate laboratory of the Henry Shaw School of Botany of Washington University, and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy.
** Southern Illinois University, Carbondale.

Issued January 29, 1958.

species are recognized in this study as valid, with only one of the entire fifteen listed by him placed in synonymy.

Between 1838 and 1890, six species were ascribed to *Stylosanthes* by various authors, but all apply to species previously named.

A more detailed revision was provided by Taubert[10] in 1890, including morphology, generic relationships, and geographical distribution in addition to keys and descriptions for the species. He retained Vogel's division of the genus into two sections and recognized 22 species, four of which he himself proposed. Fifteen of these are maintained in this study, although the specific concept has changed somewhat. It is apparent that Taubert was handicapped by the limited number of specimens available for his study.

Little was added to the genus until 1919 when Hassler[11] enumerated the species of Paraguay and added fourteen subspecies, varieties, and forms to *S. guyanensis* and *S. montevidensis*.

Blake described thirteen species between 1920 and 1926, Harms[12] added one in 1923, Macbride[13] one in 1943, and Standley and Williams[14] one in 1950. In 1943, Herter[15] split the genus into two genera, *Stylosanthes* and *Astyposanthes*, equivalent to Vogel's sections and in which rank I prefer to treat them. In the present study, 25 species are recognized, three described for the first time.

Generic Relationships

Stylosanthes belongs to the tribe Hedysareae of the papilionaceous Leguminosae characterized by monadelphous stamens and a lomentum. The alternation of subbasifixed and versatile anthers and the absence of stipels suggest its relationship with three other genera, *Zornia*, *Arachis*, and *Chapmannia*. The quartet is grouped in the subtribe Stylosanthinae.

Stylosanthes shows a close affinity with *Zornia* because of the large bracts subtending each flower and the often spicate inflorescence. The leaflets of *Zornia*, however, are paripinnate, the ovules are numerous, and bracteoles are lacking. *Arachis* is closely allied to *Stylosanthes* since both genera have similar stipules and 2–3 ovules per carpel, but they differ in that bracteoles are lacking and the loment matures underground in *Arachis*. The monotypic *Chapmannia* from Florida bears imparipinnate leaves, but differs in that it possesses minute stipules, numerous ovules per carpel, and lacks bracteoles.

Morphology

Species of *Stylosanthes* usually are herbaceous or suffruticose perennials, some attaining a height of 1.5 meters. Some species are prostrate and spreading (*S. viscosa*, some specimens of *S. hamata*), others upright and ascending. The roots usually are thick and mostly straight, with few secondary roots.

[10] Taub. in Verh. Bot. Brand. 32:1–32. 1890.
[11] Hassl. in Fedde, Rep. Sp. Nov. 16:221–223. 1919.
[12] Harms, in Fedde, loc. cit. 19:69. 1923.
[13] Macbr. in Field Mus. Publ. Bot. 13[3]:411. 1943.
[14] Standl. & L. Wms. in Ceiba 1:145. 1950.
[15] Hert. in Rev. Sudamer. Bot. 7:209. 1943.

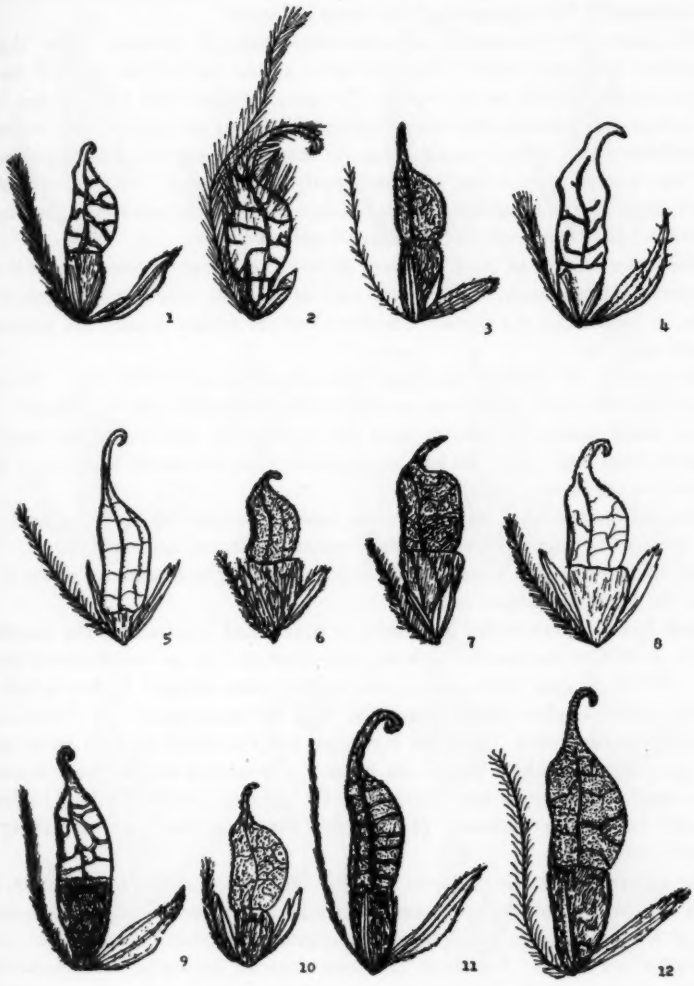

Fig. 1. Loments of *Stylosanthes*

1. *Stylosanthes capitata*, *Williams & Assis 5834*; 2. *S. bracteata*, *Jörgensen 4877*; 3. *S. calcicola*, *Small 6537* (TYPE); 4. *S. mexicana*, *Schaffner 579* (TYPE); 5. *S. erecta*, *Robertson 32*; 6. *S. scabra*, *Martius 1124*; 7. *S. scabra*, *Pickel 2556*; 8. *S. tuberculata*, *Shafer 2463*; 9. *S. sympodialis*, *Weberbauer 5936*; 10. *S. fruticosa*, *Mearns 1956*; 11. *S. subsericea*, *Standley 12110*; 12. *S. macrocarpa*, *Pringle 6721* (TYPE). All figures × 3½.

The stems are generally diffusely branched and woody at the base, rarely simple (*S. bracteata*). The indument of the stems is diverse.

The leaves of *Stylosanthes* are trifoliolate with the terminal leaflet slightly larger than the lateral ones. They are borne at the base of the cleft of the bidentate stipules. There are no stipels. The petioles range from 1.5 to 9 mm. long. The leaflets vary considerably interspecifically in shape and size. They are borne on rhachises which seldom exceed 2 mm. in length. *S. capitata* and *S. guyanensis* may have leaflets up to 4 cm. long and nearly 2 cm. broad. In most species the leaflets are elliptic to lanceolate, obtuse to acute, occasionally mucronate, and tapering to the base. Some species have black-punctate leaflets.

The upper surface of most leaflets is glabrous, although in some species it may be appressed white-hairy. The lower surface may be glabrous, puberulent, or bristly, at least along the costa. The nerves of the leaflets usually are prominent on both surfaces.

The stipules are amplexicaul, pubescent, and bidentate at the apex. They are 3- to 11-nerved, with usually one to three nerves extending into each tooth. The stipular teeth usually are shorter than the sheath. In this study, the teeth are measured from their tip to the base of the cleft while the sheath is measured from the cleft to the base of the sheath.

The inflorescence is a terminal or occasionally an axillary spike or head. In some species the inflorescence may be elongate to 20 cm. and interrupted. The number of flowers varies from one to forty or more. The flowers are sessile in the axil of the bract and adnate to it.

Each flower is surrounded by a series of bracts and bracteoles. The outermost bract is similar to the stipules in being comprised of a 3- to many-nerved sheath with a bidentate apex from which arise one or three reduced leaflets which are identical to the cauline leaflets except in size. In some species (*S. bracteata*, *S. capitata*, *S. angustifolia*), the leaflet is reduced and the sheath is often much larger than the stipular sheaths. Within the bract is a somewhat smaller outer bracteole which usually is 3-nerved and ciliate along its margin. Inside this may be found a densely ciliate axis rudiment (§ STYLOSANTHES) or this may be lacking (§ ASTYPOSANTHES).

The nature of the axis rudiment has been the subject of much conjecture, but studies show it probably to be the vestige of a secondary floral axis. In some specimens of *S. bracteata*, the axis rudiment is adnate to the outer bracteole for about one-third of its length. Essentially the same situation occurs in *Vicia monanthos*, according to Svenson.[16] Within the axis rudiment are one (§ ASTYPOSANTHES) or two (§ STYLOSANTHES) inner bracteoles which often are deeply cleft and usually long-ciliate near the apex.

The calyx is comprised of an elongated tube expanded into five lobes at the apex. The lobes usually are unequal, with one larger than the others or rarely with two larger. Usually the four smaller lobes are connate. The largest lobe usually

[16] Sven. Am. Jour. Bot. 33:394–498. 1946.

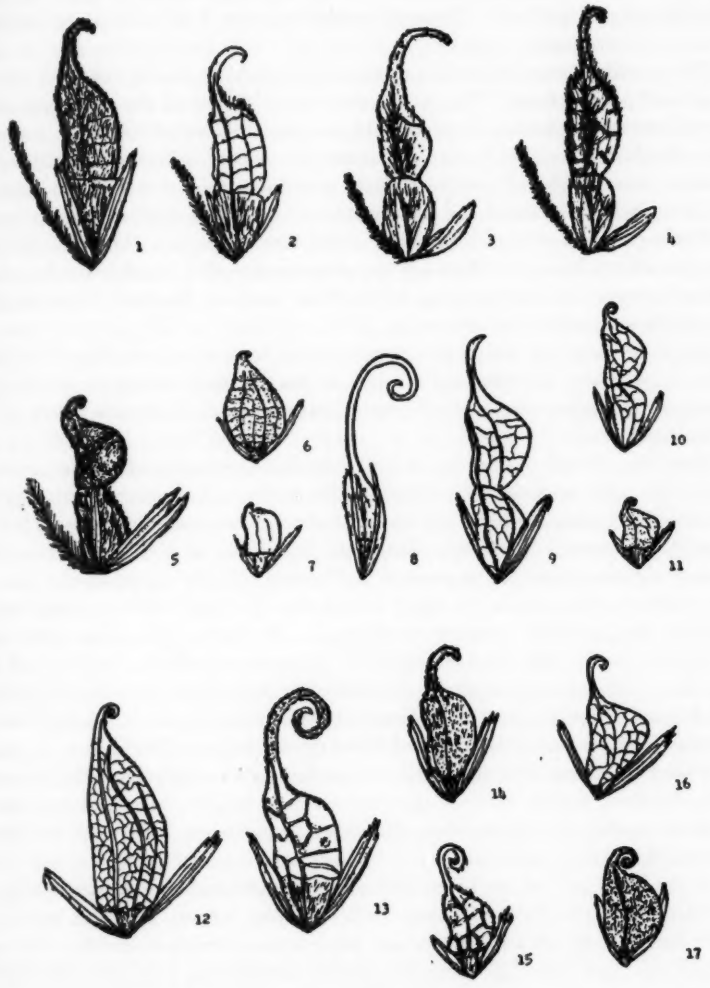

Fig. 2. Loments of *Stylosanthes*

1. *S. nervosa, Weberbauer 6215* (TYPE); 2. *S. hamata, Ricksecker 47*; 3. *S. hamata, Blake 7792*; 4. *S. hamata, Leonard 8797*; 5. *S. sericeiceps, Jahn 678* (TYPE); 6. *S. biflora, Fisher s. n.*; 7. *S. guyanensis, Martius 1123*; 8. *S. angustifolia, Burchell 9004*; 9. *S. leiocarpa, Herter 89069*; 10. *S. cayennensis, Broadway 972* (TYPE); 11. *S. viscosa, Miers 2963*; 12. *S. macrosoma, Hassler 7606*; 13. *S. humilis, Orcutt 4447*; 14. *S. figuerosa, Figueroa 897* (TYPE); 15. *S. humilis, Palmer 25*; 16. *S. hippocampoides, Herter 85562*; 17. *S. montevidensis, Venturi 9957*. All figures × 3½.

is acute, the others obtuse or subacute. They may be puberulent or glabrous. The tube generally is glabrous. The entire calyx may be 4–15 mm. long, the tube being 3–12 mm. long.

The corolla is typically papilionaceous. The petals are usually yellow or yellow-orange and purple-striate. They are inserted near the apex of the calyx tube. The standard sometimes attains a length of 10 mm. and a width of 8 mm. It is invariably suborbiculate. The wings are somewhat shorter and narrower than the standard, usually clawed and auriculate, sometimes spurred within at the base. The keel petals are incurved and subrostrate and are slightly smaller than the wings.

The stamens are monadelphous and united into a tube which becomes split, at least partially, with age. There are ten stamens, five with small versatile anthers alternating with five bearing larger sub-basifixed anthers. The staminal tube arches into and is enclosed by the keel petals.

The single carpel has a minute terminal stigma, an elongate, usually curved style which is persistent in fruit, and a subsessile ovary which contains two or rarely three campylotropous ovules borne on marginal placentae. Only one or two of the ovules develop.

The fruit of *Stylosanthes* is a bi-articulate loment terminated by the persistent style. The upper articulation is almost always fertile, the lower abortive or fertile. The lower articulation usually is densely pilose or glabrescent (*S. mexicana*, *S. leiocarpa*, *S. cayennensis*, *S. erecta*). The upper is glabrous or puberulent to sericeous or minutely tuberculate (*S. guyanensis*). The fruit usually is prominently nerved. The persistent style crowns the upper articulation as a beak which is minute or up to 8 mm. long, straight, uncinate, or circinate. The beak is glabrous or puberulent to densely villous. The relative lengths of the upper articulation and the beak are diagnostic. The upper articulation is measured from its base to a ventral protuberance formed where the upper articulation narrows into the beak. The beak, whether erect, declined, or coiled, is measured from the ventral protuberance to its maximum height as a simple vertical projection of the upper articulation. This measurement, therefore, usually does not represent the gross length of the beak but merely the distance that it projects above the upper articulation. The seeds are black, compressed, ovoid, estrophiolate.

In the latter part of the nineteenth century, a statement crept into the literature attributing two kinds of flowers to *Stylosanthes biflora*: apetalous ones from which the seeds are set exclusively, and petalous ones which are sterile. This apparently has been copied by numerous authors through the years and still persists in some of our more recent manuals. No evidence of apetalous flowers occurring in *S. biflora* was found in this study.

Geography of the Genus

The genus *Stylosanthes* is indigenous to savannas and similar areas in the eastern United States, Central America, the Antilles, South America to northern Argentina, the Galapagos Islands, central and southern Africa, Madagascar, and southern

India and Ceylon. In addition, S. *humilis* is adventive in Malaysia and Australia.

All eleven species of § ASTYPOSANTHES occur in the Western Hemisphere. Some are wide-ranging and show considerable variability, although most are well defined. Five of the seven widely distributed species of *Stylosanthes* belong in this section. S. *biflora* is rather abundant over the eastern United States. The very widespread S. *guyanensis* with its two subspecies occurs from Central America to southern Brazil and Bolivia. S. *viscosa* occurs from Baja California through Central America and northern South America and the Caribbean basin. S. *montevidensis* and its close local relatives, S. *hippocampoides* and S. *macrosoma*, center in southern Brazil, Bolivia, and Paraguay. S. *angustifolia* occurs rather frequently in northern Brazil and the Guianas. The other three species of this section, S. *cayennensis*, S. *figueroae*, and S. *leiocarpa*, are local, the first two being restricted to extreme northern South America, the last to Uruguay, Paraguay, and southeastern Brazil.

The fourteen species of § STYLOSANTHES, on the other hand, are exceedingly difficult to distinguish and are mostly restricted. Only S. *hamata* of the Antilles and S. *fruticosa* of southern Africa, India, and Ceylon are widespread. S. *scabra* is rather abundant from Colombia to Minas Geraes, Brazil. S. *macrocarpa* and S. *subsericea* are confined to Central America and S. *calcicola* to Florida, the Antilles, and parts of Central America. From Colombia and Venezuela to Peru and Ecuador are found S. *mexicana* (also in Mexico and Bolivia), S. *nervosa*, S. *tuberculata* (also in the Antilles), S. *sericeiceps*, and S. *sympodialis* (also in the Galapagos Islands). S. *bracteata* and S. *capitata* center in Brazil. S. *erecta* occurs in east-central Africa.

Uses

Certain species of *Stylosanthes* (S. *fruticosa*, in particular) are used as fodder crops. In Australia, S. *guyanensis* ssp. *guyanensis* has been planted in an effort to check soil erosion. Nodules of nitrogen-fixing bacteria are present on the roots of most of the species. Data for some specimens indicate *Stylosanthes* to be a good cover crop for coffee.

Several folk uses are attributed to certain members of the genus. Taubert noted that a few species have been used as diuretics. Hutchinson and Dalziel[17] attribute many uses for S. *erecta* by native Africans:

> In Gambia an infusion of the plant is taken internally for colds, etc. In N. Nigeria the odorous smoke produced in a pipe is blown on to arrow wounds as an antidote to their poison. The plant is a common ingredient in superstitious herbal practice, *e.g.*, the root worn as a charm or prepared as a wash is a preventive of injury by sharp weapons (Hausa *maganin k'arfe*, literally "medicine against metal"). Other plants with hard roots are similarly employed (*e.g.*, *Uraria picta*). It is an ingredient in aphrodisiac prescriptions. A decoction of the root or leaf used as a daily bath for an infant will enable him to walk very early. The plant, smoked like tobacco, and also made into a decoction, is a charm against injury by a blow by a cudgel, and will cause the weapon to break.

[17] Appendix to Fl. W. Trop. Afr. p. 262. 1937.

ACKNOWLEDGMENTS

The author is grateful to Dr. Robert E. Woodson, Jr., who supervised the study and who meticulously criticized the manuscript; to Dr. Edgar Anderson and the staff of the Missouri Botanical Garden for the courtesies extended to him; and to his many friends and colleagues who utilized the keys and descriptions and added numerous invaluable comments.

SYSTEMATIC TREATMENT

STYLOSANTHES Sw. Prod. Veg. Ind. Occ. 108. 1788. (T: S. *hamata* (L.) BSP.)

Astyposanthes Hert. in Rev. Sudamer. Bot. 7:209. 1943.

Herbs, rarely subshrubs. Leaves pinnately 3-foliolate; stipules amplexicaul, divided at the apex into two teeth, adnate to the base of the petioles; stipels none. Inflorescence spicate, terminal or axillary, 1- to several-flowered; flowers yellow or orange with purple stripes; calyx 5-lobed and with a long tube; corolla 5-merous, papilionaceous; stamens 10, the filaments united into a tube which splits with age, with 5 versatile anthers alternating with 5 sub-basifixed anthers; fruit a 1- to 2-articulated loment; seeds ovoid, light brown to black, smooth, lustrous.

The herbaria in which the cited specimens are deposited and their abbreviations are as follows: Chicago Natural History Museum (F), Gray Herbarium (GH), Missouri Botanical Garden (MO), New York Botanical Garden (NY), and the United States National Herbarium (US).

KEY TO THE SPECIES

Sect. I. STYLOSANTHES. Each flower, or at least the lower flowers, subtended by an axis rudiment; inner bracteoles 2 (1 in *S. sericeiceps*).

A. Bracts 13–25 mm. broad, with 13–23 conspicuous and usually broad, colored nerves.
B. Fertile articulations of the loment often 2, the upper glabrous, the beak less than one-third as long as the upper articulation, glabrous or with a very few short stiff hairs; nerves of the bracteal sheath about 15; stems usually with scattered bristles. Brazil, Venezuela.....1. *S. capitata*
BB. Fertile articulations of the loment 1, pilose, the beak only slightly shorter than the upper articulation, pilose; nerves of the bracteal sheath about 21; stems pilosulous to villous. Brazil, Paraguay.....2. *S. bracteata*
AA. Bracts at most 10 mm. broad, with fewer than 15 nerves which are inconspicuous.
C. Beak of the loment straight or only slightly curved; leaflets glabrous on both surfaces (rarely with marginal cilia); teeth of the upper stipules mostly longer than the sheath. Florida, Central America, Mexico, Bahamas, Cuba.....3. *S. calcicola*
CC. Beak of the loment uncinate or coiled; leaflets usually pubescent, at least on the lower surface (occasionally glabrous in *S. erecta* of Africa and *S. hamata* of the West Indies); sheath of the upper stipules mostly longer than the teeth.
D. Loment completely glabrous or with some pubescence on the beak only or occasionally on the nerves in *S. mexicana*.
E. Stems sericeous or bristly; leaflets sparsely but conspicuously bristly-ciliate; loment often green, with both articulations usually fertile; inflorescence obovoid. Mexico, Venezuela, Bolivia.....4. *S. mexicana*
EE. Stems glabrous or puberulent above; leaflets without bristly cilia; loment brown, with only one articulation usually fertile; inflorescence often narrow. West Africa.....5. *S. erecta*
DD. Loment pubescent on the body and usually on the beak.
F. Stem and bracts bearing tuberculate-based hairs (sometimes merely with tubercles); lower surface of leaflets usually villous with interspersed tuberculate bristles; beak

of the loment shorter than the upper articulation (sometimes equaling it in *S. macrocarpa* and *S. nervosa*).

G. Beak of the loment half to one-third the length of the upper articulation.

H. Bracts shortly scabrous-hispid; inflorescence usually nearly as broad as long; beak of the loment short-hairy.

I. Leaflets often punctate beneath, obtuse; stem bearing short dark setae, the whole aspect of the plant dingy brown; fertile articulation usually 1, pubescent throughout. Brazil, Ecuador, Venezuela, Colombia, Bolivia. ....6. *S. scabra*

II. Leaflets not punctate beneath, acute; stem setose or puberulent to densely pilose, not dingy brown; fertile articulations often 2, pilosulous only on the ribs. Bahamas, Cuba, Colombia, Venezuela, Peru....7. *S. tuberculata*

HH. Bracts villous or with long tuberculate bristles; inflorescence often 2–3 times longer than broad; beak of the loment usually rufous-pilose.

J. Bracts softly villous and rarely with tuberculate bristles; inflorescence 2–3 times longer than broad; loment 1.0–1.5 mm. broad, the beak rufous-pilose. Ecuador, Peru, Galapagos Islands....8. *S. sympodialis*

JJ. Bracts with tuberculate bristles; inflorescence about as broad as long; loment 1.5–2.5 mm. broad, the beak puberulent. Africa, Ceylon, India. ....9. *S. fruticosa*

GG. Beak nearly equaling to exceeding the upper articulation.

K. Beak of the loment strongly coiled; bracteal sheath and often the stem sericeous and with interspersed tuberculate bristles. Honduras, Mexico.... ....10. *S. subsericea*

KK. Beak of the loment curved to strongly uncinate; bracteal sheath and stem with tuberculate bristles but not sericeous.

L. Upper articulation and beak combined about 8 mm. long, the beak about equaling the upper articulation; plants to 0.2 m. tall. Mexico....11. *S. macrocarpa*

LL. Upper articulation and beak combined 5.0–7.5 mm. long, the beak sometimes slightly shorter than the upper articulation; plants to 1 m. tall.

M. Fertile articulations mostly 2; bracteal sheath usually bearing long tuberculate-based bristles; leaflets elliptic, obtuse to subacute, usually puberulent. Africa, Ceylon, India....9. *S. fruticosa*

MM. Fertile articulation usually 1; bracteal sheath short-hispid to densely ciliate; leaflets usually oblanceolate, acute to acuminate, glabrous or occasionally hispid beneath. Venezuela, Peru, Bolivia, Argentina. ....12. *S. nervosa*

FF. Stem and bracts pilose, villous, or nearly glabrous, lacking tuberculate bristles; lower surface of leaflets pilose or appressed-villous or glabrous, never with tuberculate bristles; beak of the loment equaling or exceeding the upper articulation (except *S. sericeiceps*).

N. Beak of the loment equaling or exceeding the upper articulation; pubescence of the bracteal sheath whitish; stem usually not pubescent throughout. Florida, Bahamas, Cuba, Central America, Colombia, Venezuela....13. *S. hamata*

NN. Beak of the loment about one-half as long as the upper articulation; pubescence of the bracteal sheath tan or rufous; stem often pubescent throughout.

O. Loment pubecsent throughout; leaflets glabrous above, 15–25 mm. long; bracteal sheaths tan-pilose. Venezuela....14. *S. sericeiceps*

OO. Loment pubescent above, glabrous below; leaflets minutely pubescent above, 20–40 mm. long; bracteal sheaths rufous-pilose. Peru, Ecuador, Galapagos Islands....8. *S. sympodialis*

Sect. II. ASTYPOSANTHES. Flowers not subtended by an axis rudiment; inner bracteole 1.

A. Beak of the loment minute, at most about one-fifth as long as the upper articulation, the fertile articulation 1.

B. Fertile articulation shortly hairy throughout or rarely glabrous, terete, 2.5–3.0 mm. long. Eastern United States....15. *S. biflora*

BB. Fertile articulation minutely tuberculate near the apex or rarely with a few scattered appressed white hairs, flattened, 1.5–3.0 mm. long. Bahamas, Central America, Mexico, South America....16. *S. guyanensis*

AA. Beak of the loment from one-fourth as long to exceeding the upper articulation, the fertile articulations 1–2.

C. Leaflets 0.5–2.0 mm. broad; inflorescence very narrow and elongate; beak of the loment strongly uncinate, often 2–3 times as long as the pubescent upper articulation. Brazil, Guianas.....17. S. *angustifolia*

CC. Leaflets 2–6 mm. broad; inflorescence usually capituliform, globose to ovoid or obovoid; beak of the loment various but not strongly uncinate.

D. Loment glabrous (occasionally pubescent only on the beak).

E. Loment with 2 fertile articulations, the beak straight or uncinate; bracteal leaflets stalked.

F. Beak straight or nearly so, about equaling the upper articulation, together about 5–6 mm. long; bracts, leaflets, and stems densely short-bristly. Brazil, Uruguay, Paraguay.....18. S. *leiocarpa*

FF. Beak uncinate, one-third as long as the upper articulation, together 3.0–3.5 mm. long; bracts and sometimes the leaflets and the stems with scattered long bristles, often glabrous. French Guiana.....19. S. *cayennensis*

EE. Loment with 1 fertile articulation, the beak strongly uncinate to coiled; bracteal leaflets sessile or subsessile.

G. Loment conspicuously reticulate-nerved, about as broad as long (excluding the beak); inflorescence 4- to 8-flowered. Uruguay, Argentina.....20. S. *hippocampoides*

GG. Loment obscurely nerved, about twice as long as broad (excluding the beak); inflorescence 2- to 4-flowered. Paraguay.....21. S. *macrosoma*

DD. Loment pubescent (if nearly glabrous, the stem viscid).

H. Beak shorter than or nearly equaling the upper articulation; stem often viscid.

I. Stems with viscid hairs or short-hispid; leaflets usually punctate beneath; fertile articulations 1–2.

J. Fertile articulations usually 2, the upper decidedly widest above the middle, the beak coiled, about one-third the length of the upper articulation. Bahamas, Cuba, Central America, Mexico, South America.....22. S. *viscosa*

JJ. Fertile articulation usually 1, broadest at or below the middle, the beak nearly straight or slightly uncinate, one-half to nearly equaling the upper articulation. Colombia.....23. S. *figueroae*

II. Stems without viscid hairs; leaflets not punctate; fertile articulation 1. Brazil, Paraguay, Uruguay, Bolivia, Argentina, Colombia.....24. S. *montevidensis*

HH. Beak nearly 2–4 times longer than the upper articulation; stems not viscid. Central America, Mexico, Bahamas, Cuba, Colombia, Venezuela, Brazil.....25. S. *humilis*

Section I. STYLOSANTHES

Section *STYPOSANTHES* Vog. in Linnaea 12:68. 1838. (T: S. *hamata* (L.) Taub.)

Each flower, or at least the lower, subtended by an axis rudiment; inner bracteoles 2.

Styposanthes hamata (L.) Taub., as type of the genus, automatically becomes the type of § STYLOSANTHES.

1. STYLOSANTHES CAPITATA Vog. in Linnaea 12:70. 1838, ex char.

Stems erect, branched, to 1 m. tall, subligneous near the base, decumbent or ascending, densely and shortly white-hairy and also with some scattered bristles, the pubescence generally more dense below each node. Leaflets oblong to elliptic, to 30 mm. long and 15 mm. broad, usually about 15 mm. long and 5 mm. broad, acute and mucronulate at the apex, densely villous on both surfaces, with 7–9 pairs of conspicuous veins; petioles 3–6 mm. long, densely villous, the rhachis 1.0–3.5 mm. long; sheath of the stipules 7–9 mm. long, densely villous, longer than the subulate teeth, several-nerved. Spikes thick, capituliform, about two-thirds as broad as high, to 35 mm. long, many-flowered, on peduncles usually 5–7

cm. long, occasionally 2–3 cm. long; bracts with a single very reduced leaflet; sheath often purplish, 8–12 mm. broad, conspicuously 11- to 17-nerved, copiously soft-pubescent; outer bracteole 1, to 3 mm. long, ciliate; axis rudiment 5–7 mm. long in fruit, very long-ciliate; inner bracteoles 2, 2.0–2.5 mm. long and much narrower than the outer, densely ciliate at the apex. Calyx tube 4–6 mm. long, the mostly acute and sparsely ciliate lobes about 2.5 mm. long. Standard obovate, 5–7 mm. long; wings obovate, 4–5 mm. long, auriculate at the base; keel petals 3–4 mm. long, falcate and auriculate. Loment to 2.5 mm. broad, reticulate-nerved; both articulations usually fertile (either sometimes abortive), the upper about 3.5 mm. long and glabrous, the lower somewhat shorter and glabrous or sparsely pubescent; beak uncinate, about 1 mm. long, glabrous or with very few short stiff hairs on the inner face.

Taubert in his diagnosis of S. *capitata* states that the legume is uni-articulate, the lower joint being abortive. However, specimens of this species may bear two fertile articulations. The original description of S. *capitata* which contains no mention of the fruit apparently is based on an incomplete specimen, for Vogel comments: *"Vidi specimen unum incompletum"*.

All species of *Stylosanthes* except S. *capitata*, S. *bracteata*, and S. *angustifolia* possess 1–3 leaflets between the teeth of the bracteal sheaths. In these three, a small laminal extension of the midvein of the sheath usually is all that is present.

Specimens from Venezuela and the Piauí state of Brazil are more coarse and have the general vegetative appearance of S. *scabra*. The nature of the inflorescence and loment clearly distinguishes S. *capitata* from S. *scabra*.

Grows in fields, forests, or waste ground and is known only from Brazil and Venezuela. It grows at altitudes of about 1000 meters. Vogel does not specifically cite any specimens but merely states that S. *capitata* has been collected in Brazil by Sellow between Victoria and Bahia (fig. 3).

BRAZIL: MARANHÃO: Rio Tocantins, *Pires & Black 1994* (NY). MINAS GERAES: Belo Horizonte, *de Oliveira s. n.* (US), *Williams & Assis 5646*, *5863* (GH), *5834* (GH, MO, NY); Morro das Pedras, *Williams & Assis 6475* (GH); Pampulha, *Williams 5644* (NY). PIAUÍ: Oeiras, *Gardner 2093* (GH, NY); exact locality unknown, *Lützelburg 112* (NY).

VENEZUELA: ANZOÁTEQUI: near Mapira, *Lasser 775* (US). BOLÍVAR: Ciudad Bolívar, *Bailey 1434* (GH, NY, US).

2. STYLOSANTHES BRACTEATA Vog. in Linnaea 12:70. 1838. (T: *Sellow 4734*!)

Stems herbaceous, very slender, erect, simple or occasionally branched, to 2 dm. tall, pilosulous to villous throughout. Leaflets lanceolate to elliptic, acute to obtuse and mucronulate at the apex, to 25 mm. long and 4 mm. broad, usually much narrower, pilose on both surfaces, with 5–7 pairs of veins prominent beneath; petioles 1–2 mm. long, pilosulous, the rhachis about 0.5 mm. long; sheath of the stipules 5–8 mm. long, pilosulous or villous as the stem, 17- to 21-nerved, the teeth lance-subulate, 4.5–7.0 mm. long. Spikes capitate, 8- to several-flowered, to 30 mm. long; bracts unifoliolate, pilose and ciliate, 10–15 mm. wide, the sheaths

Fig. 3

8.0–9.5 mm. long and with 15–21 prominent purplish nerves, the teeth 2.0–3.5 mm. long, the sessile leaflet to 5.5 mm. long; outer bracteole 1, 3.0–3.5 mm. long, bifid and ciliate near the apex; axis rudiment 7–9 mm. long in fruit, very densely pilose; inner bracteoles 2, 2–3 mm. long, ciliate. Calyx tube 8.0–8.5 mm. long, the lobes 2.0–2.5 mm. long and ciliate. Standard obovate, 4.5–6.0 mm. long; wings 3.5–4.5 mm. long, auriculate at the base; keel petals 3–5 mm. long, auriculate. Loment to 2 mm. wide, reticulate-nerved; lower articulation abortive, upper articulation 3–4 mm. long, densely pilose; beak strongly uncinate, 3.0–3.5 mm. long, pilose.

The presence of the copiously and softly hairy broad bracts makes *S. bracteata* readily distinguishable from other species of the genus. This species is the most slender *Stylosanthes* and, when in fruit, possesses the longest axis rudiment. In some specimens, the axis rudiment is adnate to the outer bracteole for about one-third of its length.

In dry regions in Paraguay and southwestern Brazil at altitudes around 800 meters; may also occur in northeastern Argentina. Burkart[18] comments that specimens referable to *S. bracteata* collected by Spegazzini (*2194* and *2195*) may be from Argentina, although the labels signify only "*Norte de la provincia de Corrientes*" (fig. 3).

BRAZIL: MATO GROSSO: Capão Bonito, *Archer & Gehrt 105* (US). MINAS GERAES: Ituiutabá, *Macedo 479* (US), *1241* (MO); Uberaba, *Regnell s. n.* (US). PARANÁ: between Lagos and Desiro, *Dusén 15684* (GH); Tibagu, *Reiss s. n.* (F); Villa Velha, Ponta Grossa, *Hoehne 23369* (GH, NY). WITHOUT PRECISE LOCALITY: Rio Vardo, *Riedel s. n.* (NY); *Sellow 4734* (GH, F).

PARAGUAY: Estancia Primera, *Jörgensen 4877* (US, MO); between Río Apa and Río Aquidaban-mi, *Fiebrig 5208* (GH, US); Tapiracuay River, *Hassler 4363* (GH, NY); exact locality unknown, *Hassler 8510* (NY).

3. STYLOSANTHES CALCICOLA Small, Man. Southeast. Fl. U. S. 730. 1932. (T: *Small, Mosier, & Small 6537*!)

Stems erect, to 0.5 m. tall, branched from near the base, minutely pubescent along one side, or sometimes glabrous, rarely pubescent throughout. Leaflets lanceolate to ovate, acute or acuminate at the apex, to 15 mm. long, glabrous or ciliate on margins near the base, with 3–5 pairs of conspicuous veins; petioles 2–4 mm. long, glabrous or puberulent, the rhachis 0.2–1.0 mm. long; sheath of the stipules glabrous or puberulent, with about 7 conspicuous nerves extending into the usually somewhat longer teeth. Spikes narrowly oblong or ovoid, 0.5–1.5 cm. long, crowded, 2- to several-flowered; bracts unifoliolate, the sheath equaling to twice as long as the teeth, averaging 4 mm. wide, ciliate and often bristly on the back, 5- to 7-nerved; outer bracteole 1, about 3 mm. long, ciliate at the apex; axis rudiment 6.0–7.5 mm. long in fruit, sparsely pilose; inner bracteoles 2, 2.0–2.5 mm. long, ciliate at the apex. Calyx tube 3–4 mm. long, about 1 mm. longer than the acute lobes. Standard obovate, 4.5–6.0 mm. long; wings 4–5 mm. long, auriculate; keel petals falcate, 3.5–4.5 mm. long. Loment 1.5–2.0 mm. broad, conspicuously nerved; both articulations usually fertile, the upper 2.5–3.0 mm. long, densely and shortly white-hairy or sometimes glabrate, the lower 2.0–2.5 mm. long, puberulent or sericeous; beak straight or only slightly curved, 1.5–2.5 mm. long, from half as long to equaling the upper articulation, with short white hairs or glabrous.

Stylosanthes calcicola is distinguished from all other species of the section by its straight beak and its general lack of pubescence.

Small described *S. calcicola* in 1932 from a collection made in Dade County, Florida, in 1915. All the Florida specimens were collected in pinelands in hammocks. In addition to Florida, the species is indigenous to Mexico (Yucatan), Guatemala, and Cuba. Apparently the first collection of this species was made from Yucatan by Gaumer (*908*) in 1895 or 1896. Although there are minor differences between the Florida and Yucatan specimens, the characters of the loment

[18] Darwiniana 3:327. 1939.

and the general lack of pubescence throughout the entire plant seem to indicate that these populations belong to the same species. The specimens from Florida are mostly low, much-branched plants (tall and unbranched in *Cornman 2132*) with densely pubescent loments while those from Yucatan and Cuba are considerably taller and generally possess pubescent loments. The leaflets of the Florida specimens are shorter.

Stylosanthes calcicola resembles *S. hamata* with respect to leaflet morphology, habit, and the densely pubescent loments. It is an apparent calciphile with a tolerance for rather warm, arid climates.

UNITED STATES: FLORIDA: Dade Co.: pinelands near Murden Hammock, *Small, Mosier & Small 6438* (MO); pinelands near Ross-Costello Hammock, *Small, Mosier & Small 6537* (US). Monroe Co.: Big Pine Key, *Cornman 2132* (MO).

GUATEMALA: HUEHUETENANGO: between Nentón and Las Palmas, *Steyermark 51654* (F).

MEXICO: YUCATAN: Chichancanab, *Gaumer 2044* (GH, US, MO, F); Izamal, *Gaumer 992* (GH, US, F); San Anselmo, *Gaumer 1955* (GH, NY, MO, F), *Gaumer 1956* (GH, US, MO, F), *Gaumer 908* (MO, US, F); Progreso, *Flores 1* (F).

BAHAMAS: NEW PROVIDENCE ISLAND: West Bay, *Degener 18984* (GH, NY).

CUBA: CAMAGÜEY: Ganado, Cayo Sabinal, *Shafer 863* (NY, F).

4. STYLOSANTHES MEXICANA Taub. in Verh. Bot. Brand. 32:21. 1890. (T: *Schaffner 579*!)

Stylosanthes bangii Taub. ex Rusby, in Mem. Torr. Bot. Club 4:206. 1895. (T: *Bang 936*!)

Stem ascending to spreading, subligneous near the base, to 3 dm. tall, usually much branched from near the base, densely covered with appressed white hairs, often with scattered bristles at least on the lower half of the stem. Leaflets broadly lanceolate to obovate, obtuse to subacute, glabrous or nearly so above, usually sparsely bristly-ciliate, occasionally with some tuberculate-based bristles on the lower surface, with 3–4 pairs of conspicuous veins; terminal leaflet to 16 mm. long and 4 mm. broad, the lateral leaflets somewhat smaller; petioles 3–6 mm. long, shortly white-hairy to nearly glabrous, the rhachis to 2 mm. long; sheath of the stipules equaling or exceeding the teeth, somewhat veiny, pubescent like the stem. Spikes dense, more or less oblongoid, to 15 mm. long, several-flowered; outer bracts trifoliolate, the inner unifoliolate, the sheath with short white hairs or sometimes with tuberculate-based bristles, 7- to 9-nerved, 3.5–5.0 mm. long, the teeth 0.5–1.0 mm. shorter than the sheath; outer bracteole 1, oblong-lanceolate, ciliate, bifid, 3.5–4.5 mm. long; axis rudiment to 6 mm. long in fruit, long white-ciliate; inner bracteoles 2, ciliate, 2–3 mm. long. Calyx tube to 6 mm. long, the obtuse lobes about 2–3 mm. long, usually glabrous, sometimes ciliate. Standard suborbiculate, 4.5–6.0 mm. long; wings nearly equaling the standard in length, subauriculate at the base; keel petals falcate, 3.0–4.5 mm. long. Loment 6–7 mm. long, 1.5–3.5 mm. broad, reticulate- nerved; both articulations usually fertile, the upper 3–5 mm. long, glabrous or with some appressed pilosity on the nerves when immature, the

lower somewhat shorter, glabrescent, occasionally abortive; beak recurved-uncinate or sometimes with a half-coil, 2.5–3.0 mm. long, usually about equaling the upper articulation in length, glabrous or sparsely hairy.

Stylosanthes mexicana shows much variation in leaflet shape and pubescence. While most specimens possess some tuberculate hairs in addition to simple pili, *Leavenworth 135* from Nuevo León, and *Purpus 4925* from San Luis Potosí, Mexico, lack these bristles. The leaflets of *Purpus 4925* are obtuse instead of acute.

On valley floors dissected by arroyos and alluvial fans, in wooded gorges, and savannas at altitudes from 800 to 2500 meters (fig. 3).

At first glance, the geographic distribution of S. *mexicana* seems to be very peculiar. This species is known from a few states in central Mexico and from Caracas, Venezuela, and the chacos of Bolivia, widely disjunct areas. This situation, however, occurs in several species of flowering plants, striking examples being *Larrea divaricata* (Zygophyllaceae), *Atamisquea emarginata* (Capparidaceae), and *Koeberlinia spinosa* (Koeberliniaceae). This last species is known from the Mexican states of Tamaulípas, Nuevo León, and San Luis Potosí and again from a small area in the western chacos of Bolivia.

In searching for an explanation of this seemingly unusual distribution, Johnston[19] observes that both the areas in Mexico and Bolivia are extensive regions which are characterized by low atmospheric humidity and rainfall usually less than twenty inches annually, and in which the climatic and edaphic conditions are rather similar. The plants which occur in these areas belong principally to genera of a xerophitic nature. Johnston points to the presence in the deserts of North America of floristic elements which apparently are a part of a flora now well represented in South America. He believes we are dealing "with a very old American desert flora formerly shared by both continents. In South America it is now relatively well preserved but in North America it lingers in a few recognizable remnants."

It is obvious that at the present time the extensive unbroken belt of wet tropical forest between the Mexican and Bolivian stations presents "effective barriers to the exchange of elements." Johnston postulates that "during dry, warm epochs, an exchange might have been effected along relatively arid coastal strips similar to . . . those now present in western Central America, Ecuador, and Peru."

The species from Bolivia, known as S. *bangii,* is indistinguishable from S. *mexicana* and is considered synonymous.

MEXICO: COAHUILA: Palm Canyon, *Marsh 969* (F). HIDALGO: near El Salto, *Pringle 11969* (GH, US, F). NUEVO LEÓN: Diente Canyon, near Monterrey, *Mueller & Mueller 325* (F); Monterrey, *Pringle 2253* (GH, F); Villa de Santiago, *Leavenworth 135* (MO). OAXACA: Mitla, *Smith 101* (US). QUERÉTARO: San Juan del Río, *Rose, Painter & Rose 9528* (US). SAN LUIS POTOSÍ: Mina de San Rafael, *Purpus 4928* (GH, NY, MO, F); San Miguelito, *Schaffner 800* (GH, NY), *579* (US, F). TAMAULÍPAS: Buena Vista Hacienda, *Wooton s. n.* (US); Cerro de la Tamaulipeca, *Bartlett 10608* (F), *10612* (GH, F); near Miquihuana, *Stanford, Retherford & Northcraft 793* (GH, NY, MO); vicinity of La Victoria, *Palmer 490* (GH, NY, US); exact locality unknown, *Viereck 300* (US).

BOLIVA: COCHABAMBA: Bolivian Plateau, *Bang 963* (GH, NY, MO, US, F).

[19] Jour. Arn. Arb. 21:356–363. 1940.

VENEZUELA: DISTRITO FEDERAL: Caracas, *Pittier 9679* (GH, US, NY); lower Catiza, near Caracas, *Pittier 7319* (GH, US).

5. STYLOSANTHES ERECTA Beauv. Fl. Owar. 2:28. 1807, ex char.

Stylosanthes guineensis Schum. in Schum. & Thonn. Beskr. Guin. Pl. 357. 1828, ex char.
Ononis coriifolia Reichb. ex Guil., Perr. & Rich. Pl. Senegam. 204. 1830, nom. nud. in synon.
Stylosanthes guineensis G. Don, Gen. Syst. 2:281. 1832, ex char.
Stylosanthes erecta var. *guineensis* Vog. in Linnaea 12:68. 1838, ex char.
Stylosanthes erecta var. *acuminata* Welw. ex Baker, in Oliver, Fl. Trop. Afr. 2:156. 1871, ex char. (T: *Welwitsch 2127*.)

Stems suffrutescent, suberect, 0.3–1.5 m. tall, much branched, puberulent above, glabrous below, rarely with bristles. Leaflets oblanceolate, mucronulate, narrowed at both ends, glabrous, often punctate beneath, usually with 2–5 pairs of conspicuous veins; terminal leaflet to 25 mm. long and 5.5 mm. broad, the lateral ones to 13 mm. long and 4.5 mm. broad; petioles 4–6 mm. long, glabrous or puberulent, the rhachis about 1.5 mm. long; sheath of the stipules 4.0–7.5 mm. long, glabrous, puberulent, ciliate, or bristly, 5- to many-nerved, the teeth 3.5–5.0 mm. long. Spikes oblongoid to narrowly elongate and sometimes interrupted, 4- to 12-flowered; bracts usually unifoliolate, the leaflet averaging 6 mm. long, the sheath 4–6 mm. long, 4.0–5.5 mm. broad, ciliate along the margins and often bristly on the back, 5- to 7-nerved, the teeth 2.5–4.5 mm. long; outer bracteole 1, 3–6 mm. long, ciliate at the apex; axis rudiment 3.5–6.5 mm. long, ciliate; inner bracteoles 2, 2.0–3.5 mm. long. Calyx tube 4.0–5.5 mm. long, the lobes about 2 mm. long. Standard suborbiculate, 4.0–6.5 mm. long; wings 4–5 mm. long, auriculate, clawed; keel petals falcate, 3.5–4.5 mm. long. Loment 1.5–2.0 mm. wide, reticulate and with one longitudinal nerve per face; only the upper articulation usually fertile, 3.5–4.5 mm. long, glabrous or nearly so; beak uncinate, glabrous or short-hairy on the inner face, 1.5–2.5 mm. long, less than half as long as the upper articulation.

Stylosanthes erecta is distinguished by its loments which are mostly uni-articulate and glabrous or nearly so, although the illustration which accompanies Beauvais' original description depicts a bi-articulate loment.

The shape and pubescence of the leaflets are quite variable and have given rise to two named varieties regarding which there has been considerable confusion. Taubert cites *Welwitsch 2127* under var. *guineensis*, but this specimen is the type for var. *acuminata*. Var. *guineensis* is usually applied to those specimens which have bristly stems. Although including var. *guineensis* in his 'Leguminosae of Tropical Africa', Baker[20] states that it is hardly varietally distinct from S. *erecta*. Since there is no line of demarcation with reference to degree of pubescence among the specimens, it does not seem wise to retain either variety.

The inflorescence is usually much longer than broad, often becoming interrupted, although some specimens have more ovoid and compact heads. The leaflets in some specimens are punctate beneath.

[20] Legum. Trop. Afr. 320. 1926.

In addition to the localities listed, the species is reported to occur in Sierra Leone, Angola, and Gaboon. The habitats include dry gravelly hills, sea sands, sandy pastures, and sandy thickets along rivers.

BELGIAN CONGO: Leopoldville, from Boma to Shinkakasa, *Claessens s. n.* (GH).
FRENCH WEST AFRICA: IVORY COAST: Grand Drewin, *Roberty 13710* (MO). SENEGAL: exact locality unknown, *Sieber 37* (MO, NY).
GOLD COAST: Keta, *Darko 584* (MO); "Pram and Pram", *Robertson 32* (MO).
LIBERIA: exact locality unknown, *Cook 137, 145* (US).
NIGERIA: Lagos (Apapa), *Bels 43* (MO); exact locality unknown, *Vogel s. n.* (GH).

6. STYLOSANTHES SCABRA Vog. in Linnaea 12:69. 1838, ex char.

Stylosanthes diarthra Blake, in Proc. Biol. Soc. Wash. 33:49. 1920. (T: *Jahn 169*!)
Stylosanthes gloiodes Blake, loc. cit. 45. 1920. (T: *Townsend A 57*!)
Stylosanthes plicata Blake, loc. cit. 46. 1920. (T: *Kuntze s. n.*!)

Stems suffruticose, ascending to suberect, much branched, to 1.5 m. tall, densely and shortly hairy and often setosulous, sometimes viscid, rarely glabrescent. Leaflets elliptic to oblong-lanceolate, obtuse, mucronate, densely and shortly hairy above and below, sometimes glabrescent, with a few scattered setae, with 4–5 pairs of usually conspicuous veins; terminal leaflet to 15 mm. long, 5 mm. broad, the lateral ones to 12 mm. long and 4.5 mm. broad, often punctate beneath; petioles 2.5–6.0 mm. long, canaliculate above, scabrous with dense short hairs, the rhachis 1.0–3.5 mm. long; sheath and teeth of the stipules variable in length, the sheath usually 1.5–5.0 mm. longer than the teeth, short-hispid, 7- to 9-nerved. Spikes short, crowded, oblongoid, several-flowered; bracts unifoliolate, the leaflet about 4 mm. long, hispid, the sheath 3.5–6.5 mm. long, 3.0–4.5 mm. broad, densely hispid, about 7-nerved, the teeth 2.5–4.5 mm. long and somewhat shorter than the sheath; outer bracteole 1, lanceolate, 2.0–4.5 mm. long, bifid and ciliate at the apex; axis rudiment 4–5 mm. long, ciliate; inner bracteoles 2, 2–4 mm. long, ciliate at the apex. Calyx tube 3.0–6.5 mm. long, the more or less acute lobes 1.5–3.5 mm. long. Standard broadly obovate to suborbiculate, to 7 mm. long and 6 mm. broad; wings clawed, auriculate, spurred within at the base, 4–5 mm. long; keel petals auriculate, 3.5–4.5 mm. long. Loment about 2.5 mm. broad, reticulate-nerved; upper articulation 2–4 mm. long, shortly hairy, the lower 2–3 mm. long, evenly pilose throughout; beak uncinate, shortly hairy, 1–2 mm. long, one-half to one-third as long as the upper articulation.

The species has a wide range but is apparently most abundant in the Minas Geraes area of Brazil. It is attributed to Peru by Bentham[21] (fig. 4).

Stylosanthes scabra of § STYLOSANTHES is the viscid counterpart of *Stylosanthes viscosa* of § ASTYPOSANTHES.

BOLIVIA: LA PAZ: Larecaja, *Mandon 698* (GH).
BRAZIL: BAÍA: exact locality unknown, *Salzmann s. n.* (MO). MATO GROSSO: exact locality unknown, *Kuntze s. n.* (NY, US). MINAS GERAES: Ituiutaba, *Macedo 2226* (MO); Santa Luzia, *Williams & Assis 201* (GH, MO), *Barreto 5773* (F); Serro, *Williams*

[21] In Mart. Fl. Bras. 15[2]:1. 1859.

& *Assis 6850* (GH, US). PARAÍBA: exact locality unknown, *de Moraes 887* (NY). PERNAMBUCO: Tapera, *Pickel 2556* (GH, US, NY, F), *2481* (GH, US, NY); Tiuma, *Millspaugh 67* (F); exact locality unknown, *Gardner 973* (GH, NY, US, F). RIO GRANDE DO SUL: Jacuí, *Téodoro 1783* (GH). SÃO PAULO: Campinas, *Santoro 638* (US); Avenida Barão Itapura, Campinas, *Santoro 380* (US); San José do Barreiro, *Hoehne & Gehrt 17665* (GH). WITHOUT PRECISE LOCALITY: São João Bapt., *Pohl 567* (NY).

COLOMBIA: CUNDINAMARCA: Aguadita, *Ricardo s. n.* (US). HUILA: between Hobo and Gigante, *Arbeláez & Cuatrecasas 8328* (US, F). EL VALLE: Cali, *Bermúdez 20* (US), *Killip & Cuatrecasas 38410* (US); Carretera al Mar, west of Cali, *Killip & Lehmann V 39798* (US); Cisneros, Dagua Valley, *Killip 11431* (US, GH, NY); north of Palestina, *Garcia 6328* (US); Trés Cruces, *Bermúdez & Barkley 17C869* (NY, US).

ECUADOR: Cariamanga, *Townsend A 57* (US).

VENEZUELA: MÉRIDA: Sierra de Nevada de Mérida, *Jahn 108* (US); above Los Gonzalez, *Steyermark 56234* (F). TRUJILLO: Valera, *Jahn 169* (US); Nagua, *Warming 101* (US).

7. STYLOSANTHES TUBERCULATA Blake, in Proc. Biol. Soc. Wash. 33:48. 1920. (T: *Britton 3336*!)

Stems suffruticose to 5 dm. tall, erect, branched, evenly and densely pilose and with dense short tuberculate-based hairs. Leaflets elliptic to oblong-lanceolate, acute and often mucronulate at the apex, the margins bristly-ciliate, both surfaces more or less appressed-pilose and often tuberculate-hispid at least below, with 4–6 pairs of prominent lateral nerves; terminal leaflet 10–20 mm. long, 3–5 mm. broad, the lateral ones somewhat smaller; petioles 2–4 mm. long, hispid-setose, the rhachis about 1 mm. long; sheath of the stipules 5–7 mm. long, pubescent and hispidulous as the stem, the subulate teeth 2–3 mm. long. Spikes narrowly oblongoid, 6–15 mm. long, 6- to 10-flowered; bracts unifoliolate, the leaflet pilosulous and densely tuberculate-hispid, the sheath 3.5–5.0 mm. long, hispidulous, the teeth slightly shorter; outer bracteole 1, 3–4 mm. long, bifid or entire, obtuse, ciliate or glabrous; axis rudiment 3–4 mm. long in fruit, pilose; inner bracteoles 2, 2–3 mm. long, narrow, ciliate or glabrous. Calyx tube 4–5 mm. long, glabrous, the obtuse lobes 2.5–3.0 mm. long, ciliate or glabrous. Standard 4–5 mm. long, 3–4 mm. broad; wings somewhat auriculate at the base, short-spurred within, 4–5 mm. long; keel petals falcate, 3.0–4.5 mm. long. Loment reticulate-nerved, about 2.5 mm. broad; upper articulation of the loment fertile, 3–4 mm. long, usually sparsely or occasionally densely pilosulous on the ribs, the lower articulation fertile or abortive; beak slightly uncinate, shortly hairy, at least near the base, 1.5–2.0 mm. long.

In savannas and on open banks at altitudes from 400 to 1800 meters (fig. 4).

BAHAMAS: NEW PROVIDENCE ISLAND: Southwest Landing, *Britton 3336* (US).

CUBA: CAMAGÜEY: Pueblo Romano, Cayo Romano, *Shafer 2463* (US, NY, F).

COLOMBIA: ANTIOQUIA: Medellín, *Archer 1002* (GH, US). CAUCA: La Paila, *Holton 22* (NY). HUILA: Quebrada de Angeles to Río Cabrera, *Rusby & Pennell 325* (NY); Gigante, Ancón, *Plata 72* (US). NORTE DE SANTANDER: Río Zulia, *Nicifaro s.n., 2412* (US). EL VALLE: Cali, *Fosberg 22001* (US); Dagua, *Killip 5431* (NY, GH, US); Jamundi, *Bermúdez 24* (US). WITHOUT PRECISE LOCALITY: Tocoima, *Arbeláez 2237* (US).

PERU: HUANCAVELICA: Tayacaja, below Colcabamba, valley of the Mantaro, *Weberbauer 6451* (GH, US, F).

VENEZUELA: DISTRITO FEDERAL: around Caracas, *Pittier 9754* (NY, US, GH). WITHOUT PRECISE LOCALITY: Avila, *Vogl 661* (F).

8. STYLOSANTHES SYMPODIALIS Taub. in Verh. Bot. Brand. 32:19. 1890. (T: *Spruce 6373*, photo!)

Stylosanthes psammophila Harms in Fedde, Rep. Sp. Nov. 19:69. 1923. (T: *Weberbauer 5936*!)

Stems erect, to 4.5 dm. tall, branched from near the base, shortly villous above, glabrate below, rarely with short bristles. Leaflets narrowly lanceolate to elliptic, acute at the tip, the larger ones to 40 mm. long and 5.5 mm. broad, evenly villous on both surfaces, usually with long marginal ciliá, with 4–6 pairs of moderately conspicuous veins; petioles to 10 mm. long, usually much shorter, pilose, the rhachis about 2 mm. long; sheath of the stipules covered with soft short often rufous hairs, rarely with a few bristles. Spikes few-flowered; outer bracts usually trifoliolate, the inner unifoliolate, the sheath about 2 mm. longer than the teeth, densely covered with soft often rufous hairs, rarely with tuberculate bristles, 5- to 7-nerved; outer bracteole 1, 2.5–3.0 mm. long, pilose near the apex; axis rudiment to 7 mm. long, with long rufous hairs; inner bracteoles 2, 2.0–2.5 mm. long, pilose near the apex. Calyx tube 3–5 mm. long, the acute, ciliate lobes 1–2 mm. long. Standard about 4.5 mm. long, suborbiculate; wings 3–4 mm. long, auriculate at the base; keel petals 3–4 mm. long, auriculate. Loment strongly reticulate-nerved, to 2 mm. broad; both articulations of the loment usually fertile, the upper about 3 mm. long, glabrous below, with tawny hairs above, the lower nearly as long, densely pilose; beak 2.0–2.5 mm. long, usually slightly shorter than the upper articulation, uncinate or almost with a complete coil, densely covered with short hairs.

Occurs in sandy soils on the Galapagos Islands and in Peru and Ecuador. The specimens from the Galapagos Islands have leaflets 5–15 mm. long which sometimes bear short erect hairs along with the rufous pilosity on the bracteal sheaths. The continental specimens have longer and more narrow leaflets (to 40 mm. long) and usually possess only appressed pubescence on the bracteal sheaths. These latter specimens have been determined by some as S. *psammophila*.

In his monograph of *Stylosanthes*, Taubert describes under S. *scabra* an unnamed variety from the Galapagos Islands, stating "*var. caulibus villoso-pubescentibus, non scabris.*" These specimens belong to S. *sympodialis*.

ECUADOR: GALAPAGOS ISLANDS: Abingdon Island, *Snodgrass & Heller 836* (GH); Albemarle Island, Tagus Cove, *Stewart 1695* (MO, GH, US, NY), *Snodgrass & Heller 171* (GH), *Howell 9599* (GH); Bindloe Island, *Snodgrass & Heller 767* (GH), *Baur 90* (GH); Charles Island, *Snodgrass & Heller 450* (GH), *Stewart 1697* (MO, GH, US, NY), *Baur 92* (GH), Post Office Bay, *Howell 8815* (GH, US), Black Beach, *Svenson 151* (GH, F); James Island, *Rorud 144* (GH); Jervis Island, *Baur 89* (GH); North Indefatigable Island, *Snodgrass & Heller 673* (GH); Santa Cruz Island, *Rorud 145* (GH); South Seymour Island, *Howell 9948* (US). GUAYAS: Playas, *Asplund 5086* (US); Punta Carnero, *Svenson 11301* (NY); Salinas, *Svenson 11400* (US, GH); Punta Centinella, *Svenson 11258* (NY); Salinas, La Puntilla, *Asplund 5610* (US); Salinas, *Asplund 5650* (US). PIURA: exact locality unknown, *Eggers 14798* (US). WITHOUT PRECISE LOCALITY: *Espinosa 517, 590* (US).

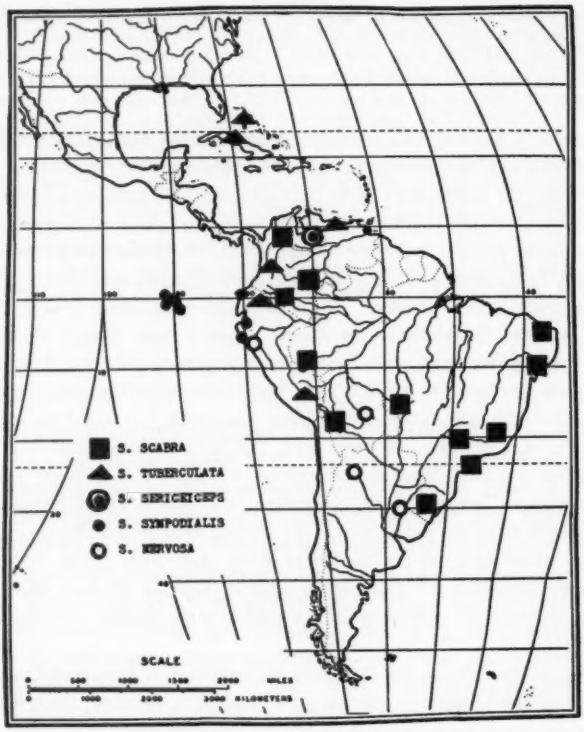

Fig. 4

PERU: PIURA: Parinas Valley, *Haught 134* (US, NY); Negritos, *Haught F 44* (NY, F); between Piura and Nomala, *Weberbauer 5936* (GH, US). TUMBES: Zarumilla, *Ferreyra 5960* (US).

9. STYLOSANTHES **fruticosa** (Retz.) Mohlenbrock, comb. nov.

Hedysarum hamatum acc. Burm. f. Fl. Ind. 167. 1768, non L.
Arachis fruticosa Retz. Obs. Fasc. 5:26. 1791, ex char.
Stylosanthes mucronata Willd. Sp. Pl. 3:1166. 1800, ex char.
Stylosanthes bojeri Vog. in Linnaea 12: 68. 1838, ex char.
Stylosanthes aprica Span. in Linnaea 15:192. 1841, ex char. (T: *Burke & Zeyher 404.*)
Stylosanthes setosa Harv. in Harv. & Sond. Fl. Cap. 2:227. 1862, ex char.
Stylosanthes flavicans Baker in Oliv. Fl. Trop. Afr. 2:156. 1871. (T: *Kotschy 425*!)

Stem suffrutescent, about 5 dm. tall, much branched, erect or spreading, sometimes prostrate, shortly white-hairy above, occasionally with scattered short bristles, these sometimes yellow, often puberulent or glabrescent below. Leaflets acute,

rarely obtuse at the tip, glabrous or puberulent to densely short-hairy, often with scattered short setae on the margins and midvein beneath, with 3–4 pairs of conspicuous nerves, or with the veins rarely obscure; terminal leaflet to 17 mm. long (rarely to 25 mm. long) and 3.0–4.5 mm. broad (rarely to 8 mm. broad), the lateral to 16 mm. long and 3.0–4.5 mm. broad; petioles 4–7 mm. long, hispidulous or shortly bristly, sometimes puberulent, the rhachis 1.0–2.5 mm. long; sheath of the stipules 4.5–10.0 mm. long, densely and shortly hairy and usually with scattered bristles, or sometimes only with bristles, with 5–7 pairs of conspicuous nerves, the subulate teeth 3–6 mm. long, never longer than the sheath. Spikes ovate, dense, 4- to 10-flowered; bracts mostly unifoliolate, the leaflet(s) often plicate, the sheath tuberculate-bristly to merely long-ciliate around the margins, 3.0–6.5 mm. long, 2.5–5.5 mm. broad, about 7-nerved, the teeth averaging 3–5 mm. long, often nearly equaling the sheath; outer bracteole 1, 4–6 mm. long, ciliate at the apex; axis rudiment 3–5 mm. long, ciliate; inner bracteoles 2, 2.5–4.5 mm. long, ciliate at the apex. Calyx tube 4.5–6.5 mm. long, the lobes 2–4 mm. long, ciliate. Standard suborbiculate, 4.5–7.0 mm. long; wings 4–5 mm. long, auriculate at the base; keel petals 4–5 mm. long, auriculate. Loment 1.5–2.5 mm. broad, reticulate; both articulations usually fertile, or the lower sometimes abortive; lower articulation, when fertile, 2.5–4.0 mm. long and as long as or slightly longer than the upper, pilose; beak somewhat uncinate or scarcely coiled, 1.5–3.0 mm. long, shortly hairy.

The specimens of *Stylosanthes* from Africa and adjacent areas which belong to § STYLOSANTHES seem to be treated best as belonging to two highly variable species: S. *erecta* from West Tropical Africa, and S. *fruticosa* from South Africa, Madagascar, India, and Ceylon. The former has loments which are glabrous or nearly so, while S. *fruticosa* possesses pubescent loments.

Stylosanthes fruticosa is extremely diverse in its morphology, and a large number of variants have been described. In this study, the only course that seemed practical was to consider all these variants as belonging to one exceedingly broad species. The basis for the deluge of species seems to be mostly the pubescence of the stems, leaves, bracts, and stipules. In all of these, however, the loment characters remain essentially uniform. Thus S. *aprica* described from Timor, S. *bojeri* from Zanzibar, S. *flavicans* from Sudan, and S. *setosa* from the Cape are being treated as S. *fruticosa*. S. *sundaica* of Malaysia, considered by most recent authors as a synonym for S. *fruticosa*, is really a synonym for a species in § ASTYPOSANTHES

Specimens collected in Kordofan by Pappi (*364*) and by Kotschy (*425*) are the basis for Baker's S. *flavicans*. These specimens are flavescent when dried and somewhat viscid and apparently represent an extreme in the S. *fruticosa* complex. Many of the bristly specimens of S. *fruticosa* are at least subviscid, however, and no dividing line may be drawn to separate the specimens. Specimens called S. *bojeri* are very bristly and are sordid upon drying. This again seems to represent only an extreme, and intergradations of all degrees of pubescence may be found.

Apparently the first mention of this species in the literature was in 1737 when

Burmann[22] recorded the polynomial '*Trifolium procumbens zeylanicum hirsutum.*' In 1768 Burmann f.[23] noted that *Hedysarum hamatum* occurred in Ceylon and Jamaica. It is evident that he included under this binomial at least two species, the present *S. hamata* (L.) Taub. from Jamaica which Linnaeus called *Hedysarum hamatum α* in 1759 and *S. fruticosa* from Ceylon. In 1791 Retzius[24] named *Arachis fruticosa* from Ceylon and included under it Linnaeus' *Hedysarum hamatum α*. Nine years later, Willdenow[25] described *S. mucronata* and listed *Arachis fruticosa* as a synonym. Therefore it appears that the first legitimate epithet to be applied to this species is *fruticosa*.

KENYA: trail from Nyeri to Wambugu, *Mearns 1956* (NY, US); 14 miles from Mombassa, vicinity of Changamme, *Mearns 2230* (US).

MOZAMBIQUE: Lourenço Marques, *Howard 56* (US), *Barle 82* (US), *Curtis 80* (GH); Lourenço Marques, Marracuene, *Quintas 6* (MO); Delagoa Bay, *Kuntze s. n.* (NY); Maputo, *Sousa 3960* (MO).

NIGERIA: on the Niger, *Baikie s. n.* (GH); exact locality unknown, *Barter 3428* (GH).

SOUTHERN RHODESIA: Matapos, *Plowes 1426* (MO); Nyamandhlovu, Plowes *1603* (MO); Umtali, *Chase 3231* (NY).

SUDAN: KORDOFAN: Nile Land, *Kotschy 425* (GH).

TANGANYIKA: Ugogo, Dodoma, *Peter 44443, 44463* (MO); Nzega, 50 miles north of Tabora, *Carnochan 10* (GH); near Manyoni, north of Kilimatinbe, *Carnochan 338* (GH); Dar-es-Salaam, *Kuntze s. n.* (NY).

UNION OF SOUTH AFRICA: TRANSVAAL: Barberton, *Thorncroft 1913* (NY); near Crocodile Poont, *Dyer & Verdoorn 3426* (NY); Pretoria, *Mogg 14785* (US). ZULULAND: Somkele, *Wood 9291* (US).

CEYLON: exact locality unknown, *Thwaites 1451* (GH, NY).

EAST INDIES: exact locality unknown, *Wight 814* (NY).

INDIA: Mysore and Carnatic, *Thompson s. n.* (GH); Salem, Hosur, *Yeshoda 415* (NY).

10. STYLOSANTHES SUBSERICEA Blake, in Proc. Biol. Soc. Wash. 33:50. 1920. (T: *Purpus 7152*!)

Stylosanthes scoparia Standl. & L. Wms. in Ceiba 1:145. 1950. (T: *Williams & Molina 11261*!)

Stems suffruticose, usually erect, slender to robust, to 1 m. tall, often much branched, long-pilose and usually sericeous throughout, occasionally with a few bristles near the inflorescence, sometimes glabrescent. Leaves crowded, the leaflets lanceolate, acuminate, the terminal to 20 mm. long and 4.5 mm. broad, the lateral to 15 mm. long and 3.5 mm. broad, shortly white-hairy on both surfaces with occasional bristles below, with 3–5 pairs of conspicuous veins often forming a submarginal nerve; petioles 5–7 mm. long, densely white-hairy, the rhachis 1.5–2.0 mm. long, pubescent as the petioles; sheath of the stipules 5–9 mm. long, sericeous with occasional scattered tuberculate-based bristles, 9- to many-nerved, the teeth lance-subulate, 6.0–7.5 mm. long. Spikes narrow, oblongoid, 4- to 10-flowered, 12–20 mm. long, on peduncles 0.5–4.0 mm. long; bracts unifoliolate, often short-

[22] Burmann, Thes. Zeyl. 1737.
[23] Burmann f., Fl. Ind. 167. 1768.
[24] Retz. Obs. Bot. Fasc. 5:26. 1791.
[25] Willd. Sp. Pl. 3:1166. 1800.

bristly on the back, 4.0–5.5 mm. wide, the sheath 4.0–5.5 mm. long and 7- to 9-nerved, the teeth 3.5–5.0 mm. long; outer bracteole 1, 4–7 mm. long, pilose nearly throughout; axis rudiment about 6 mm. long in fruit, long-ciliate; inner bracteoles 2, 3–4 mm. long, ciliate. Calyx tube 6–8 mm. long, the lobes 3–5 mm. long, the upper two lobes obtuse and long-pilose, the lateral ones similar but somewhat shorter, the lowest acute, pilose. Standard suborbiculate, 5–8 mm. long; wings mostly obovate and with a short claw, auriculate, shortly spurred, 4–6 mm. long; keel petals 3.5–5.0 mm. long, spurred within at the base. Loment about 2.5 mm. wide, conspicuously reticulate; both articulations usually fertile, the lower 3–4 mm. long and densely long-pilose, the upper 3.5–4.0 mm. long, sometimes slightly exceeding, sometimes slightly shorter than the lower, covered with long white hairs; beak 2.5–5.0 (–7.0) mm. long, white-hairy, with a distinct coil.

Stylosanthes subsericea is the woodiest member of the genus and sometimes attains a height of one meter. The circinate beak of the pubescent loment nearly equals or surpasses the upper articulation in length. The lower leaves fall early, leaving the stem bearing only the persistent subulate stipules near the base.

All the Honduran specimens previously have gone under the binomial *S. scoparia*. However, the great similarity of floral structure and vegetative characters of the Honduran plants with *S. subsericea* of Mexico indicates these two epithets to refer to the same species. The Mexican plants lack tuberculate bristles on the lower surface of the leaflets.

The species is very local and is known only through a few collections from Honduras and Oaxaca, Mexico, where it grows in regions of dry rocky hillsides and dry ravines, usually with pines and oaks, at elevations between 600–850 meters.

HONDURAS: COMAYAGUA: vicinity of Comayagua, *Standley & Chacon 5866* (F), *5400* (F). MORAZÁN: Río Yeguare, near El Zamorano, *Standley & Molina 4631* (F); Quebrada de Santa Clara, near Río Yeguare, *Standley & Williams 1598* (F); above El Zamorano, between Jicarito and El Pedregal, *Standley 12260* (F); along Río Yeguare, east of El Zamorano, *Standley 14593* (F); San Francisco, *Williams & Molina 13220* (F); Tatumbla, *Rodríguez 509* (F); Santa Inés, *Rodríguez 478* (F); Río Yeguare, *Rodríguez 973* (F); Las Mesas, *Standley 21222* (F); Quebrada de Santa Clara, *Standley & Williams 1563* (F); above El Jicarito, *Standley 21112* (F); Río Yeguare valley, Santa Clara Creek, *Williams & Molina 11261* (GH, F); near Las Mesas, *Standley 28654* (US); Río Yeguare, between Tatascan and Maraita, *Molina 4079* (US); Camino Viejo between Suyapa and Tegucigalpa, *Standley 14213* (US, F); near Río Yeguare, below El Zamorano, *Standley 12110* (MO, F); Río Capa Rosa, El Zamorano, *Rodríguez 3662* (US, F); Quebrada de Santa Clara, near Río Yeguare, *Standley & Williams 1634* (US, F); along Río Yeguare, east of El Zamorano, *Standley 1077* (US, F). EL PARAÍSO: Quebrada de Dantas, on road between Las Mesas and Yuscarán, *Standley 14983* (MO, F); vicinity of Güinope, *Standley, Williams, Molina & Padilla 2077* (F); south of Güinope, *Standley 14862* (F); Río Yeguare, *Molina 1681* (F); Caleras, *Williams & Molina 14133* (F).

MEXICO: OAXACA: Cerro de Picacho, *Purpus 7152* (GH, NY, US, MO, F); near Oaxaca, *Rose & Hough 4584* (US).

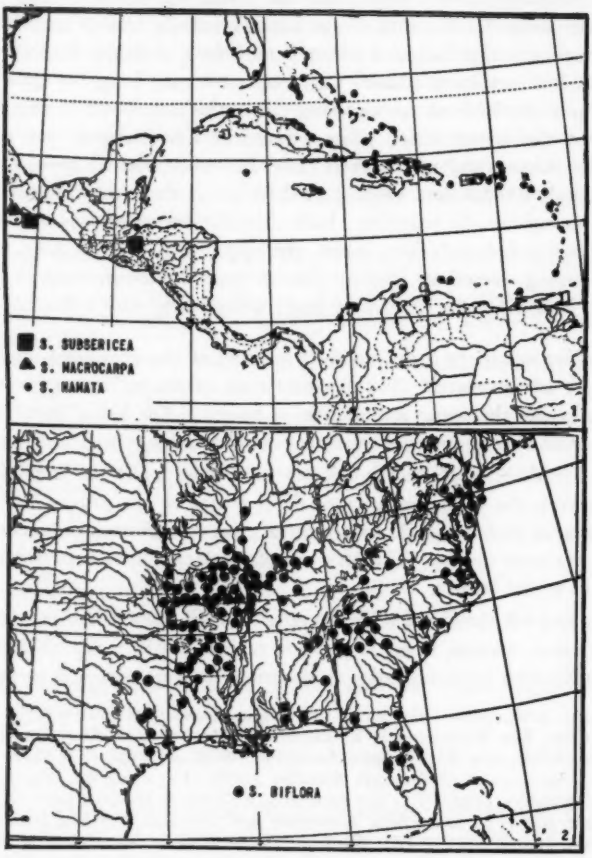

Fig. 5

11. STYLOSANTHES MACROCARPA Blake, in Proc. Biol. Soc. Wash. 33:47. 1920. (T: *Pringle 6721*!)

Stems herbaceous throughout, much branched from the base, spreading or ascending, to 20 cm. tall, densely covered with mostly appressed-ascending pili, with short tuberculate bristles beneath each node. Leaflets elliptic, subacute, mucronate, light green, glabrous above, sparsely bristly on the midvein beneath and along the margins, with 3–4 pairs of conspicuous veins; terminal leaflet to 13 mm. long and 3.5 mm. broad; petioles 3–5 mm. long, sparsely pilose and often shortly bristly, the rhachis 1.0–2.5 mm. long; sheath of the stipules about equaling the teeth, 3–4 mm. long, pubescent like the stem. Spikes ovoid, to 15 mm. long, 5- to 10-flowered; outer bracts trifoliolate, the inner unifoliolate, the sheath pilose and bristly, 6–8

mm. long, about twice as long as the teeth, 7-nerved; outer bracteole 1, oblong, about 4.5 mm. long, ciliate near the apex; axis rudiment to 8 mm. long in fruit, long-hairy; inner bracteoles 2, 2.5–3.0 mm. long. Calyx tube 5–6 mm. long, the obtuse lobes 2–3 mm. long. Standard obovate, not clawed, about 6 mm. long; wings auriculate below and shortly appendaged within; keel petals falcate. Loment 6.0–8.5 mm. long, 3.0–3.5 mm. broad, reticulate; usually only the upper articulation fertile, 4.0–4.5 mm. long, evenly appressed-pilosulous, the lower abortive or occasionally fertile, densely pilose; beak strongly uncinate, evenly appressed-pilosulous, 3.5–4.0 mm. long, usually equaling the superior articulation.

Stylosanthes macrocarpa, known only from hills near Oaxaca, Mexico, closely resembles *S. mexicana* but differs in fruit morphology. The loment of *S. macrocarpa* is evenly appressed-pilosulous throughout while that of *S. mexicana* is glabrous or puberulent only along the nerves.

The flowers examined show two inner bracteoles although Blake,[26] in his original description, states the number of "bractlets" (= inner bracteoles) to be 1, a character not in keeping with the other members of § STYLOSANTHES. One of the large sub-basifixed anthers in some of the flowers is about twice as large as the other four. This seems to be only a sporadic anomaly.

MEXICO: OAXACA: near Oaxaca, *Pringle 5782* (GH); Monte Albán, *Pringle 372* (GH).

12. STYLOSANTHES NERVOSA Macbr. Field Mus. Publ. Bot. 13[3]:411. 1943. (T: *Weberbauer 6215*!)

Stems suffrutescent, to 1 m. tall, erect, branched, usually villous with interspersed tuberculate-based hairs, at least when young. Leaflets oblong-lanceolate, acute to acuminate, glabrous or nearly so above, puberulent beneath with occasional tuberculate hairs (at least on the costa), with 4–6 pairs of conspicuous nerves, the terminal leaflet to 20 mm. long and 3 mm. broad, the lateral somewhat smaller; petioles 2–4 mm. long, pilose with occasional tuberculate hairs, rarely glabrous, the rhachis about 1 mm. long; sheath of the stipules about 7 mm. long, usually equaled by the subulate teeth, pilose, glabrate, with 5–7 nerves. Spikes narrowly oblong-lanceolate, 2- to 8-flowered; bracts unifoliolate, the leaflet ciliate, the sheath 5–7 mm. long, with numerous tuberculate hairs, densely ciliate, 5- to 7-nerved, the teeth usually 3–5 mm. long, sometimes bearing tubercles; outer bracteole 1, 4–5 (–7) mm. long, ciliate at the apex; axis rudiment 3–4 mm. long, ciliate; inner bracteoles 2, 3–4 mm. long, ciliate at the apex. Calyx tube about 7 mm. long, the lobes 3 mm. long, the upper 4 obtuse, ciliate or glabrous. Standard 5–6 mm. long; wings somewhat auriculate at the base, shortly spurred within; keel petals 3.5–5.0 mm. long, falcate. Loment about 2 mm. broad, reticulate; only the upper articulation usually fertile, about 3.5 mm. long, evenly pilose throughout; beak about 2.5 mm. long, pilose, strongly uncinate but usually not completely coiled.

[26] In Proc. Biol. Soc. Wash. 33:47. 1920.

Infrequent over a broad range, known only from a few stations in Venezuela, Peru, Bolivia, and northern Argentina (fig. 4).

ARGENTINA: CORRIENTES: exact locality unknown, *Ibarrola 2310* (US). SALTA: La Merced, *Venturi 5136* (GH, US).
BOLIVIA: SANTA CRUZ: Buena Vista, *Steinbach 5397* (NY, GH).
PERU: CAJAMARCA: Jaen, near mouth of Chinchipe River, *Weberbauer 6215* (NY, GH, US, F).
VENEZUELA: Serranias de Terepaima, *Saer 631* (F).

13. STYLOSANTHES HAMATA (L.) Taub. Verh. Bot. Brand. 32:22. 1890.

Hedysarum hamatum a L. Syst. Nat. 10:1170. 1759, ex char.
Stylosanthes procumbens Sw. Prod. Veg. Ind. Occ. 108. 1788, ex char.
Stylosanthes humilis Rich. ex Hemsl. in synon., Biol. Centr. Am. Bot. 1:272. 1882, ex char.
Stylosanthes eriocarpa Blake, Contrib. U. S. Nat. Herb. 24:4. 1922. (T: *Blake 7792*!)

Stems ascending, spreading, prostrate, or matted, to 1 m. tall, often much branched, usually with a line of fine pubescence on one side of the stem, sometimes glabrous near the base or rarely throughout, or occasionally sericeous throughout. Leaflets lanceolate to elliptic, obtuse to subacute, to 20 mm. long and 6 mm. broad, glabrous or shortly pilose above and below, with 3–6 pairs of conspicuous veins; petioles 2–6 mm. long, puberulent or pilose, the rhachis 0.5–2.5 mm. long; sheath of the stipules shortly hairy, sericeous, or glabrous, 3- to 11-nerved, usually exceeding or occasionally surpassed in length by the teeth. Spikes rather small, ovoid to oblongoid, few- to 15-flowered; outer bracts trifoliolate, inner usually unifoliolate, very variable in pubescence of the sheath, mostly only ciliate, the sheath 5- to 7-nerved; outer bracteole 1, 2.5–5.0 mm. long, ciliate at the apex; axis rudiment 2–7 mm. long; inner bracteoles 2, 2.5–3.5 mm. long, ciliate at the apex. Calyx tube 4.0–7.5 mm. long, at least twice as long as the more or less acute and ciliate lobes. Standard 4–5 mm. long, suborbiculate; wings 3.5–4.5 mm. long, clawed and auriculate; keel petals 3.0–4.5 mm. long, falcate. Loment about 2 mm. broad, reticulate; both articulations usually fertile, the upper 2–4 mm. long, glabrous or puberulent in localized areas, or densely and evenly sericeous, the lower, when fertile, somewhat shorter, pilose or glabrescent; beak equaling to exceeding the upper articulation, glabrous or with short pubescence, uncinate.

Stylosanthes hamata is readily distinguished by a series of characters which includes a more or less puberulent bi-articulate loment with a beak slightly exceeding the upper articulation and a general lack of tuberculate bristles.

This species appears to be related most nearly to S. *fruticosa* of Africa and, indeed, the two were not separated by such early authors as Burmann f. and Retzius. *Stylosanthes fruticosa* usually possesses tuberculate bristles and evenly pilosulous loments. *Stylosanthes hamata* is similar to S. *sympodialis* but in the latter the beak of the loment is shorter than the upper articulation.

The spikes are usually 2- to 5-flowered, but some specimens from the Antilles have large dense spikes which may bear as many as 15 flowers. The habit of this species may be erect to ascending, or prostrate and matted. This difference seems

to be correlated with altitude; the specimens from elevations between 100 and 900 meters tend to be upright while those near sea level seem to be matted. These latter have been known as S. *procumbens*.

The range of S. *hamata* is broad and includes Florida, eastern Mexico and Central America, the Antilles, Colombia, and Venezuela, often becoming a pest in gardens in Jamaica, Cuba, and neighboring islands.

UNITED STATES: FLORIDA: Dade Co.: *Moldenke 778* (MO).

BAHAMAS: ANDROS ISLAND: Spaniard Creek, *Small & Carter 8882* (F, NY, GH, US); Mastic Point, *Brace 7097* (NY, F); road to Little Creek, *Brace 5245* (NY). CAICOS ISLANDS: South Caicos, *Wilson 7637* (GH, NY, F); Jacksonville, *Millspaugh & Millspaugh 9100* (NY, F). CROOKED ISLAND: Marine View Hill, *Brace 4635* (NY, F); Landrail Point, *Brace 4678* (NY, F). ELEUTHERA ISLAND: Current, *Coker 339* (NY). GRAND BAHAMA ISLAND: Eight Mile Rocks, *Britton & Millspaugh 2454* (GH, NY, US, F). GRAND TURK ISLAND: The Wells, *Millspaugh & Millspaugh 9342* (NY, US, F); Waterloo, *Millspaugh & Millspaugh 9034* (F). GREAT RAGGED ISLAND: exact locality unknown, *Wilson 7821* (GH, NY, F). NEW PROVIDENCE ISLAND: Nassau, *Hitchcock s. n.* (MO, F); Clifton Point, *Degener 18985* (GH, NY, MO); Nassau, *Northrop & Northrop 37* (GH, NY, F), *Curtiss 9, 118* (GH, US, NY, MO, F), *Coker 541* (NY), near Fort Fincastle, *Wright 86* (GH, NY, F), off Soldier's Road, *Wright 223* (GH, NY), road to Lake Cunningham, *Britton 93* (NY), west of Bay Street Road, *Millspaugh 2172* (F); exact locality unknown, *Brace 444* (F). RUM CAY: Port Nelson, *Brace 3934* (NY, F). SAN SALVADOR ISLAND: exact locality unknown, *Wilson 7359* (NY, F).

CUBA: CAMAGÜEY: Pueblo Romano, Cayo Romano, *Shafer 2499* (NY). HABANA: Habana, *Palmer & Riley 821* (US), *Babs 460* (NY); Regla, *Shafer 104*; Playa de Cojimar, *Hitchcock s. n.* (F); Marianão, *Piper 6089* (US). ORIENTE: Santiago, Morro Hill, *Millspaugh 1077* (US, F), *Howard 5788* (GH, US, NY, MO); Guantánamo Bay, *Britton 1941* (US, NY); Holguin to Cacocum, *Shafer 1551* (US, NY); Santiago, *Havard 105* (NY); Santiago, Morro Castle, *Havard 82* (NY); Santiago, *Underwood & Earle 1682* (NY). WITHOUT PRECISE LOCALITY: Triscornia, *Hitchcock s. n.* (F).

DOMINICAN REPUBLIC: BARAHONA: Los Patos, *Abbott 1767* (US); Barahona, *Howard & Howard 8413* (GH, NY), *Fuertes 211* (GH, MO, NY, US, F), *von Türckheim 2804* (NY). SAN JUAN; near San Juan de la Maguana, *Howard & Howard 8795* (GH); El Cercado, Juan Santiago, Hondo, *Howard & Howard 9293* (NY). SANTIAGO: Santiago, *Jiménez 473* (US). SANTO DOMINGO: Monción, banks of Río Mao, *Valeur 802* (US); Guayubin, *Abbott 937a* (US), *942* (US); near Puerto Liberatador, Manzanillo Bay, *Howard & Howard 9659* (NY); Monción, *Valeur 248* (NY, US, MO, F); Ciudad Trujillo, *Allard 14350* (US), *13087* (US, F), *13114* (US), *13107* (US), *13313* (US), *13725* (US, MO), *14007* (US), *14281* (US); Azua, *Rose, Fitch & Russell 4028* (US, NY). WITHOUT PRECISE LOCALITY: Moca, *Ekman NH 11270* (US); Haina, *Faris 38* (US, NY); Llanos de Rafael, *Eggers 1920* (NY, US); Constanza, *von Türckheim 2529* (NY).

GRAND CAYMAN: South Sound, *Kings GC 69* (MO); Bodden Bay road, *Millspaugh 1335* (F).

HAITI: ARTIBONITE: vicinity of Ennery, *Leonard 8798* (GH, US, NY, MO), *8797* (F), *9463* (US); Gros Morne, *Leonard 9858* (US); St. Marc, *Leonard 2863* (US), *2881* (US). GONAIVES: Gonaives to La Hotte Rochée on road to Terre Neuve, *Nash & Taylor 1545* (NY). GONAVE ISLAND: Étroit, *Leonard 3401* (GH, US). MIREBALAIS: exact locality unknown, *Cook, Scofield & Doyle 81* (US). DU NORD: St. Michel de l'Atalaye, *Leonard 7037* (US); Plaisance to Marmelade, *Nash 678* (NY). NORD-OUEST: Jean-Rabel, *Leonard & Leonard 12925* (US); Port-de-Paix, *Leonard & Leonard 11001* (GH, US); vicinity of Bombardopolis, *Leonard & Leonard 13448* (NY, US). SUD: west of Jérémie, *Holdridge 928* (US). LA VALLÉE: Tortuga Island, *Leonard & Leonard 11224* (US, MO), *15583* (US). WITHOUT PRECISE LOCALITY: Plaine Centrale, Pavane-Papaye, *Ekman H6013* (US); La Cumbre, *Raunkaier 1137* (US).

JAMAICA: Sherwood Forest, *Orcutt 3137* (MO); Port Morant, *Hitchcock s. n.* (MO); Kingston, *Hitchcock s. n.* (MO); near Port Antonio, *Fredholm 3054* (US, NY); Trelawny, Jackson Town, *Hunnewell 19781* (GH); Waterloo Road, *Campbell 6019* (NY); vicinity of Mandeville, *Brown 107* (NY).

LESSER ANTILLES: ANEGADA: exact locality unknown, *Britton & Fishlock 1007* (US, NY, F). ANGUILLA: exact locality unknown, *Boldingh 5536* (NY). ANTIGUA: St. Johns, *Shafer 36* (NY); exact locality unknown, *Hutson s. n.* (US). BARBADOS: Waterford, St. Michael, *Dash 281* (US, NY, F); Codrington, *Borrell 281* (US); Hastings, *Waby 62* (US). BONAIRE: exact locality unknown, *Boldingh 7246* (NY). CURAÇAO: Santa Cruz, *Britton & Shafer 3013* (NY). GRENADA: Richmond Hill, *Broadway s. n.* (US, NY). GUADELOUPE: Pointe-à-Pitre, *Hammarlund 18* (NY); exact locality unknown, *Questel 1459* (US). INAGUA: Salt Pond Hill, *Fairchild 2599* (US); Matthew Town, *Nash & Taylor 1069* (NY, F). MONA: exact locality unknown, *Stevens 6224* (NY), *6344* (NY). ST. BARTHÉLEMY: Gustavia, *Questel 116* (NY), *217* (NY); exact locality unknown, *Forsström s. n.* (F). ST. CROIX: Corn Hill, *Ricksecker 216* (GH, MO, NY, US, F); Judith's Ferry, *Thompson 482* (GH, NY); Bassin, *Ricksecker 47* (US, MO, F). ST. JAN: Bethania to Rosenberg, *Shafer 232* (US, NY). ST. KITTS: near Basseterre, *Britton & Cowell 729* (US, NY). ST. THOMAS: Svenson's Bay, *Britton 280* (NY); Paradise Bay, *Britton & Britton 208* (US, NY). TORTOLA: Sea Cow Bay, *Britton & Shafer 667* (GH, NY). VIRGIN GORDA: exact locality unknown, *Fishlock 163* (GH, NY).

LITTLE CAYMAN: South Side, Blossom Point, *Kings LC 75* (MO).

PUERTO RICO: Quebradillas, *Stevenson 5887* (US); Guanica, *Sintenis 3756* (NY, US); Yauco, *Underwood & Griggs 658* (US, NY); Guayama, Pozuelo, *Goll 531* (US); Cayey, south of Caguas, *Heller & Heller 328* (US, NY, F); Bayamon, *Sintenis 1092* (US, MO, NY); Condado, *Britton, Britton & Brown 5764* (US, NY).

GUATEMALA: IZABAL: trail from Los Amates to Izabal, *Blake 7792* (GH, US); Puerto Barrios, *Standley 25126* (NY, US).

PANAMA: COCLÉ: Penonomé, *Shafer 36* (NY).

COLOMBIA: ATLÁNTICO: Salgar, around Puerto Colómbia, *de Kattah, Molina & Barkley Ato25* (US), *Ato48* (US); Barranquilla, *Elias 927* (US); Puerto Colombia, *Dugand 4008* (US). BOLÍVAR: La Popa, *Killip & Smith 14067* (NY, GH, US, F); Cartegena, *Molina & Barkley Bo048* (US). CUNDINAMARCA: east of Apulo, *Killip, Dugand & Jaramillo 38164* (US). MAGDALENA: exact locality unknown, *Castañeda 252* (MO). TOLIMA: Curvas de Gualanday, *Arbeláez & Cuatrecasas 6506* (US).

VENEZUELA: FALCÓN: Adicora, Paraguaná, *Tomayo 750* (US), *977* (US, F). NUEVA ESPARTA: Island of Margarita, *Miller & Johnston 68* (GH, NY, US, MO, F).

14. STYLOSANTHES SERICEICEPS Blake, in Contrib. U. S. Nat. Herb. 20:524. 1924. (T: *Jahn 678!*)

Stems suffruticose, erect, to 0.5 m. tall, densely covered with shortly appressed silvery hairs, glabrescent below. Leaflets lanceolate, to 25 mm. long and 5 mm. broad, acuminate, mucronate, usually glabrous above, minutely pubescent beneath and along the margins, with 4–7 pairs of prominent veins; petioles to 6 mm. long, sericeous, the rhachis to 2.5 mm. long; sheath of the stipules about as long as the teeth, densely short-hairy, with 3 veins crowded near the center. Spikes oblongoid or obovoid, about 15 mm. long, crowded, several-flowered; outer bracts often trifoliolate, inner unifoliolate, the sheath 5–7 mm. long, about equaling the teeth, densely covered with long tawny hairs, 5-nerved; outer bracteole 1, bifid, ciliate, about 4 mm. long; axis rudiment to 4 mm. long, densely pilose; inner bracteole 1, about equal in length to the outer but narrower. Calyx tube to 7 mm. long, the more or less pilose lobes obtuse or acute, about 3 mm. long. Standard to 8 mm. long, suborbiculate; wings 4.5–6.5 mm. long, auriculate; keel petals 4.5–6.0 mm. long, falcate. Loment 1.5–2.0 mm. broad, reticulate; both articulations fertile or

the lower sometimes abortive, the upper 2.5–3.0 mm. long, evenly clothed with short silvery hairs, the lower, when fertile, nearly 4 mm. long, pilose; beak 1.5–2.0 mm. long, nearly half as long as the upper articulation, strongly uncinate, densely white-hairy.

Stylosanthes sericeiceps apparently marks the transition between § STYLOSANTHES and § ASTYPOSANTHES in that only the lowest 2–3 flowers in each spike possess an axis rudiment and that each flower, in addition, is subtended by only one inner bracteole, the latter character one which is found throughout § ASTYPOSANTHES. The absence of the axis rudiment in upper flowers has been noted for some specimens in other species of § STYLOSANTHES (S. *hamata* and S. *subsericea*), but this is the only species in which this is combined with the absence of one of the inner bracteoles.

Stylosanthes sympodialis closely resembles S. *sericeiceps*, differing from it in the rufous villosity of the bracteal sheaths and in the unevenly pubescent loment.

There are no data as to the habitat of this species, except that it grows at altitudes between 400 and 1000 meters. It is known only from Venezuela.

VENEZUELA: MÉRIDA: Lagunillas, *Jahn 678* (US, GH, NY); between Estangues and Pointe Real, *Pittier 12842* (NY, US).

Section II. ASTYPOSANTHES (Herter) Mohlenbrock, stat. nov.

Sect. *Eustylosanthes* Vog. in Linnaea 12:63. 1838.
Astyposanthes Herter, in Rev. Sudamer Bot. 7:209. 1943.

None of the flowers subtended by an axis rudiment; inner bracteole 1.

In the absence of previous typification, *Stylosanthes humilis* HBK. is designated as the type for § ASTYPOSANTHES.

15. STYLOSANTHES BIFLORA (L.) BSP. Prelim. Cat. N. Y. Pl. 118. 1883.

Trifolium biflorum L. Sp. Pl. 773. 1753, ex char.
Arachis aprica Walt. Fl. Carol. 183. 1788, ex char.
Stylosanthes elatior Sw. in Svenska Vet. Akad. Handl. 11:296. 1789, ex char.
Stylosanthes hispida Michx. Fl. Bor. Am. 2:75. 1803, ex char.
Stylosanthes hispida var. *hispidissima* Michx. loc. cit. 1803, ex char.
Stylosanthes hispida var. *nudiuscula* Michx. loc. cit. 1803, ex char.
Stylosanthes hispida α *erecta* Pursh, Fl. Am. Sept. 2:480. 1814, ex char.
Stylosanthes hispida β *procumbens* Pursh, loc. cit. 1814, ex char.
Stylosanthes elatior β *hispidissima* Torr. & Gray, Fl. N. Am. 1:354. 1838, ex char. (T: *Michaux s. n.*)
Stylosanthes biflora α *elatior* O. Ktze. Rev. Gen. 1:209. 1891, ex char.
Stylosanthes biflora β *guianensis* O. Ktze. loc. cit. 1891, ex char.
Stylosanthes riparia Kearney, in Bull. Torr. Bot. Club 24:565. 1897. (T: *Kearney 674*!)
Stylosanthes biflora var. *hispidissima* Poll. & Ball, in Proc. Biol. Soc. Wash. 13:134. 1900, ex char.
Stylosanthes biflora var. *hispidissima* Mohr, in Contrib. U. S. Nat. Herb. 6:570. 1901, ex char.
Stylosanthes floridana Blake, in Proc. Biol. Soc. Wash. 33:51. 1920. (T: *Sudworth s. n.*!)
Stylosanthes riparia var. *setifera* Fern. in Rhodora 40: 438. 1938. (T: *Fernald & Long 8321*!)
Stylosanthes riparia f. *ochroleuca* Fern. loc. cit. 1938. (T: *Fernald & Long 8732*!)

Stems herbaceous to subligneous at the base, to 6 dm. tall, erect or spreading, much branched or rarely sparsely branched, glabrous to puberulent to densely hispid, the bristles sometimes yellowish. Leaflets ovate to elliptic to lanceolate, obtuse to acute at the tip, glabrous on both surfaces and occasionally with spinulose teeth on the margins, sometimes punctate beneath, with 3–6 pairs of nerves; terminal leaflet to 40 mm. long and 10 mm. broad, usually much smaller, the lateral ones slightly smaller than the terminal; petioles 1–3 mm. long, glabrous to puberulent to hispidulous, the rhachis 0.5–1.5 mm. long; sheath of the stipules 3–10 mm. long, glabrous to puberulent to densely hispid, with numerous nerves, the subulate teeth 3–8 mm. long, often setose. Spikes small, 1- to 8-flowered; bracts mostly unifoliolate or the outer sometimes trifoliolate, the sheath puberulent to densely hispid, rarely glabrous, 3.0–6.5 mm. long, 2.5–5.5 mm. broad, mostly 5- to 9-nerved, the teeth usually somewhat shorter; outer bracteole 1, lanceolate, 2–3 mm. long, glabrous to ciliate at the apex; axis rudiment none; inner bracteole 1, 1.0–2.5 mm. long, glabrous to ciliate at the apex. Calyx tube 2.5–5.0 mm. long, glabrous, the more or less acute lobes 2–4 mm. long, glabrous to puberulent. Standard suborbiculate, 4.5–7.0 mm. long, to 5.5 mm. broad; wings 3.5–4.5 mm. long, auriculate, spurred within at the base; keel petals denticulate to entire at the apex, auriculate, spurred within at the base. Loment 2.5–3.0 mm. broad, strongly reticulate with vertical nerves; only the upper articulation of the loment fertile, 2.5–5.0 mm. long, obovoid, plump, puberulent throughout; beak 0.5–1.0 mm. long, coiled.

The *Stylosanthes biflora* complex is defined as including populations not only of S. *biflora* but also S. *riparia* and S. *floridana* of other authors. The members of this complex are relatively constant with respect to loment characters but are diverse in leaflet shape, pubescence, and to some extent habit. However, some variation may occur in shape of the loments with some articulations more inflated than others, or in degree of reticulation. Loments are generally puberulent although they may become glabrous with age. Degree of maturity affects such characters of the loment so that in some specimens, the entire range of variability may be observed.

Most authors refer specimens with acute leaflets and without bristles on the stem to S. *biflora* (L.) BSP., and those with acute leaflets and bristles on the stem and bracteal sheaths to S. *biflora* var. *hispidissima* (Michx.) Pollard & Ball. Specimens with obtuse leaflets and which may be either non-bristly or bristly are regarded mostly as S. *riparia* Kearney or its variety *setifera* Fern., respectively. Specimens from the extreme southeastern United States which lack bristles completely are known sometimes as S. *floridana* Blake. A sharp line of demarcation among these variants is, however, difficult to determine, a fact which has been noted previously by some workers (Isely[27]).

Supposedly the best criterion to separate S. *riparia* from S. *biflora* is the position of the beak on the upper articulation of the loment. In S. *riparia*, the beak is said to

[27] Iowa State Coll. Jour. Sci. 30:113. 1955.

be oriented terminally on the loment rather than at one side as in S. *biflora*. However, in most specimens identified as S. *riparia*, the beaks appear lateral. Isely attributes the differences between fruits to "artifacts of observation" since "the degree to which the beak is or is not symmetrically placed may depend on the angle from which it is viewed".

Other varieties or species which have been segregated from S. *biflora* seem only to represent extremes.

UNITED STATES:

ALABAMA: DeKalb Co.: *Ruth 338* (MO). Lee Co.: *Baker s. n.* (MO). Marshall Co.: *Hubricht B 1667* (MO). Mobile Co.: *Graves 961* (MO).

ARKANSAS: Baxter Co.: *E. J. Palmer 5961* (MO). Clark Co.: *Demaree 17794* (MO). Craighead Co.: *Demaree 3495* (MO). Cross Co.: *Demaree 19618* (MO). Dallas Co.: *Demaree 23350* (MO), *23340* (MO). Drew Co.: *Demaree 18016* (MO). Franklin Co.: *Demaree 17788* (MO). Hot Springs Co.: *Demaree 17463* (MO). Jefferson Co.: *Demaree 19460* (MO). Johnson Co.: *Demaree 19966* (MO). Lincoln Co.: *Demaree 19156* (MO). Logan Co.: *Demaree 17682* (MO). Miller Co.: *Heller & Heller 4126* (MO). Prairie Co.: *Demaree 22303* (MO). Pulaski Co.: *Demaree 17293* (MO). Saline Co.: *Demaree 21195* (MO). Sharp Co.: *Emig 168* (MO). Union Co.: *Demaree 19421* (MO). Yell Co.: *Demaree 21270* (MO).

DELAWARE: Newcastle Co.: *Commons s. n.* (MO). Sussex Co.: *Churchill s. n.* (MO).

FLORIDA: Duval Co.: *Curtiss 6418* (MO). Escambia Co.: *Brinker 473* (MO). Hillsborough Co.: *Ferguson s. n.* (MO). Jefferson Co.: *Hitchcock s. n.* (MO). Lake Co.: *Nash 1309* (MO). Marion Co.: *Woodson & Schery 97* (MO). Volusia Co.: *Hood s. n.* (MO).

GEORGIA: Bulloch Co.: *Harper 946* (MO). Cobb Co.: *Duncan 8646* (MO). DeKalb Co.: *Miller, Perry, Boyd & Myers 531* (MO). Gwinnett Co.: *Allard 129* (MO). Madison Co.: *Duncan 11588* (MO). Oconee Co.: *Small s. n.* (MO). Stephens Co.: *Duncan 11737* (MO). Union Co.: *Duncan 7835* (MO). Whitfield Co.: *Harper 393* (MO).

ILLINOIS: Jackson Co.: *Mohlenbrock 5058* (MO).

KANSAS: Cowley Co.: *White 134* (MO). Montgomery Co.: *Rydberg & Imler 454* (MO).

KENTUCKY: McCreary Co.: *Wherry & Pennell 13873* (MO). Whitley Co.: *Wherry & Pennell 13843* (MO).

LOUISIANA: Rapides Parish: *Ball 621* (MO).

MARYLAND: Montgomery Co.: *Painter 1084* (MO).

MISSOURI: Barry Co.: *Bush 3265* (MO). Benton Co.: *Steyermark 24436* (MO), *24436a* (MO). Butler Co.: *Steyermark 11489* (MO). Callaway Co.: *Steyermark 26175* (MO). Camden Co.: *Steyermark 20655* (MO). Cole Co.: *Steyermark 14981* (MO). Crawford Co.: *Steyermark 15373* (MO). Dade Co.: *Steyermark 5653* (MO). Dent Co.: *Kellogg 995* (MO). Douglas Co.: *Steyermark 15373* (MO). Dunklin Co.: *Bush 6271* (MO). Franklin Co.: *Craig s. n.* (MO). Greene Co.: *Dewart 72* (MO). Henry Co.: *Steyermark 15948* (MO). Hickory Co.: *Steyermark 24488* (MO). Howell Co.: *Blankinship s. n.* (MO). Iron Co.: *Pammel s. n.* (MO). Jasper Co.: *Palmer 461* (MO). Jefferson Co.: *Steyermark 1366* (MO). Lincoln Co.: *Steyermark 8130* (MO). McDonald Co.: *Palmer 6a* (MO). Maries Co.: *Steyermark 15303* (MO). Marion Co.: *Davis 7866* (MO). Oregon Co.: *Palmer & Steyermark 41740* (MO). Pike Co.: *Steyermark 25893* (MO). Polk Co.: *Steyermark 23987* (MO). Ralls Co.: *Steyermark 25865* (MO). Reynolds Co.: *Steyermark 14201* (MO). Ripley Co.: *Mackenzie 327* (MO). St. Louis Co.: *Drushel 4311* (MO). Shannon Co.: *Bush s. n.* (MO). Stoddard Co.: *Steyermark 20763* (MO). Stone Co.: *Steyermark 22699* (MO). Taney Co.: *Palmer 5888* (MO). Vernon Co.: *Drouet 130* (MO). Wayne Co.: *Steyermark 11217* (MO). Webster Co.: *Steyermark 23897* (MO). Wright Co.: *Bush s. n.* (MO).

New Jersey: Burlington Co.: *Meredith s. n.* (MO). Camden Co.: *Martindale s. n.* (MO). Gloucester Co.: *Parker 12430* (MO). Hunterdon Co.: *Fisher s. n.* (MO). Middlesex Co.: *Mackenzie 2871* (MO). Ocean Co.: *Churchill s. n.* (MO). Salem Co.: *Meredith s. n.* (MO).

North Carolina: Cherokee Co.: *Fox 4034* (MO). Cumberland Co.: *Fox & Godfrey 2600* (MO). Edgecombe Co.: *Fox 4080* (MO). Harnett Co.: *Fox & Godfrey 2559* (MO). Henderson Co.: *Davis 9030* (MO). Hoke Co.: *Schallert s. n.* (MO). Orange Co.: *Wilson 28* (MO). Rowan Co.: *Heller 14005* (MO). Swain Co.: *Beardslee & Kofoid s. n.* (MO). Wayne Co.: *Fox, Godfrey & Boyce 4325* (MO).

Oklahoma: Caddo Co.: *Goodman 2342* (MO). Choctaw Co.: *Houghton 4025* (MO). Comanche Co.: *Stevens 1411* (MO). Johnston Co.: *Palmer 6438* (MO), *6438a* (MO). McCurtain Co.: *Houghton 3788* (MO). Payne Co.: *Stratton 188* (MO). Woods Co.: *White 277* (MO).

Pennsylvania: Bedford Co.: *Berkheimer 3458* (MO). Lancaster Co.: *Eisenhower s. n.* (MO). Montgomery Co.: *Redfield 1524* (MO). Philadelphia Co.: *Eby s. n.* (MO). Schuylkill Co.: *Collector Unknown* (MO). York Co.: *Glatfelter s. n.* (MO).

South Carolina: Aiken Co.: *Eggert s. n.* (MO). Anderson Co.: *Davis 8441* (MO). Dillon Co.: *Godfrey SC49040* (MO). Georgetown Co.: *Godfrey 146* (MO). Laurens Co.: *Davis s. n.* (MO). Oconee Co.: *Duncan 11255* (MO). Pickens Co.: *Rodgers 385* (MO).

Tennessee: Cocke Co.: *Kearney 675* (MO); *Kearney 674* (MO).

Texas: Bowie Co.: *Eggert s. n.* (MO). Brazos Co.: *Palmer 11750* (MO). Dallas Co.: *Reverchon 193* (MO). Harris Co.: *Boon 185* (MO). Lee Co.: *Eggert s. n.* (MO). Nacogdoches Co.: *Parks RX2287* (MO). Parker Co.: *Tracy 8025* (MO). Travis Co.: *Buckley s. n.* (MO). Waller Co.: *Hall 153* (MO).

Virginia: Smyth Co.: *Small s. n.* (MO).

West Virginia: Jackson Co.: *Berkley 816* (MO). Lincoln Co.: *Berkley 899* (MO). Summers Co.: *Fox 2481* (MO).

16. Stylosanthes guyanensis (Aubl.) Sw. Svenska Vet. Akad. Handl. 11:296. 1789.

Stems herbaceous or mostly suffruticose, erect or rarely scandent, to 1 m. tall, glabrous to puberulent to pilose or often hispid or setose, the setae often purplish. Leaflets green to purple, lanceolate to elliptic to nearly ovate, acute or occasionally obtuse at the apex, glabrous to puberulent to tuberculate-bristly, particularly on the margins and the costa beneath, sometimes spinulose-toothed, with 2–7 pairs of nerves, the terminal usually 5–30 mm. long and 2–10 mm. broad (rarely to 45 mm. long and 20 mm. broad), the lateral ones slightly smaller than the terminal; petioles 1–10 mm. long, sometimes canaliculate above, glabrous to puberulent to setose, the rhachis 0.5–1.5 mm. long; sheath of the stipules glabrous to pilose to setose, 2–15 mm. long, 3- to many-nerved, the subulate teeth 2–10 mm. long. Spikes small, narrow, and 2-flowered to large, globose, and about 40-flowered; bracts mostly unifoliolate, the leaflet sometimes much reduced and often spinulose-toothed, the sheaths green to purple, glabrous to puberulent to bristly, 3–7 mm. long, 3- to 9-nerved; outer bracteole 1, lanceolate or ovate, 2.5–3.0 mm. long, acuminate, glabrous to pilose, occasionally purplish at the apex; axis rudiment none; inner bracteole 1, 2–3 mm. long, acuminate, glabrous to pilose, colored like the outer bracteole. Calyx tube 4–8 mm. long, glabrous to sparsely pubescent, the

lobes 3–5 mm. long, obtuse to acute, ciliate or sometimes pilose. Standard 4–8 mm. long, 3–5 mm. broad, suborbiculate; wings 3.5–5.0 mm. long, auriculate, spurred within at the base; keel petals 3.5–5.0 mm. long, falcate. Loment 1.5–2.5 mm. broad, reticulate; only the upper articulation fertile, glabrous to minutely short-pubescent near the apex, or occasionally with sessile glands near the apex, ovoid, plump, 2–3 mm. long; beak minute, 0.1–0.5 mm. long, strongly inflexed.

KEY TO THE SUBSPECIES

a. Leaflets green, usually 10–60 mm. long, sometimes tuberculate-bristly but not spinulose-toothed; internodes usually much greater than 1.5 cm. long; inflorescence mostly 5- to 40-flowered. Central America, South America.....16a. S. *guyanensis* ssp. *guyanensis*

aa. Leaflets purplish, 4–12 mm. long, densely and shortly tuberculate-bristly on the margin and the costa, appearing short-serrate; internodes 0.5–1.5 cm. long; inflorescence 1- to 4-flowered. Mexico.....16b. S. *guyanensis* ssp. *dissitiflora*

Stylosanthes guyanensis is a most variable species. The leaflets range from small and lanceolate to large and elliptic. The indument of the stem is diverse. The spikes are large and to 40-flowered to small and 1- to 2-flowered. Numerous subspecies, varieties, and forms have been proposed, but intergradations occur between almost all. Except for subspecies *dissitiflora*, there is no strong geographical correlation with any of the variants. A great number of the most southern specimens are 40-flowered and bristly and the northern specimens 5- to 20-flowered and more or less viscid, but this is far from constant.

Great confusion as to the proper name for this species has arisen. Aublet described *Trifolium guyanense* as having pubescent loments and illustrated it thus. The type photograph, however, appears to coincide with many of the specimens examined in this study with glabrous or puberulent loments. Those considering Aublet's *T. guyanense* as inapplicable to present known specimens employ the binomial S. *gracilis* for this broad species.

Numerous other morphological extremes have been proposed: S. *hispida* Rich. with densely hispid stems; S. *surinamensis* Miq. with rather narrow leaflets; S. *ruellioides* Benth. with densely pubescent stems and broad leaflets; S. *longiseta* Micheli with the stems bearing long bristles; and S. *pohliana* Taub. with acuminate leaflets. *Stylosanthes ingrata* Blake from Vaca Falls, British Honduras, is without fruit but seems to be S. *guyanensis* ssp. *guyanensis*.

Stylosanthes guyanensis ssp. *guyanensis* occurs from Central America through South America into northern Argentina, also in the Antilles. It has been planted in Australia in an effort to impede soil erosion. *Stylosanthes guyanensis* ssp. *dissitiflora* is limited to a small area in southwestern Mexico. It occurs at altitudes between 3500 and 5000 feet.

16a. STYLOSANTHES GUYANENSIS ssp. GUYANENSIS

Trifolium guyanense Aubl. Pl. Guian. 776. 1775, ex char. (T: *Aublet s. n.*, photo!)
Stylosanthes hispida Rich. Act. Soc. Hist. Nat. Par. 2:112. 1792, ex char.
Stylosanthes gracilis HBK. Nov. Gen. et Sp. 6:507. 1823, ex char.
Stylosanthes surinamensis Miq. in Linnaea 18:567. 1844, ex char.
Stylosanthes ruellioides Benth. in Mart. Fl. Bras. 15[1]:90. 1859, ex char.
Stylosanthes guyanensis β *subviscosa* Benth. loc. cit. 92. 1859, ex char.
Stylosanthes longiseta Micheli, in Mem. Soc. Phys. Genève 28:7. 1883, ex char.
Stylosanthes pohliana Taub. in Verh. Bot. Brand. 32:29. 1890. (T: *Pohl 1997*!)
Stylosanthes guyanensis var. *pubescens* Pilger, in Engl. Bot. Jahrb. 30:160. 1901, ex char. (T: *Pilger 286*).
Stylosanthes juncea f. *intermedia* Chod. & Hass. in Bull. Herb. Boiss. ser. 2, 4:884. 1904. (T: *Hassler 3781*).
Stylosanthes montevidensis var. *longiseta* (Micheli) Chod. & Hass. loc. cit. 885. 1904. (T: *Hassler 4573*).
Stylosanthes guyanensis var. *genuina* Hass. in Fedde, Rep. Sp. Nov. 16:220. 1919. (T: *Hassler 7781*!)
Stylosanthes guyanensis var. *genuina* f. *esetosa* Hass. in Fedde, loc. cit. 221. 1919. (T: *Hassler 2834*!)
Stylosanthes guyanensis var. *intermedia* (Vog.) Hass. in Fedde, loc. cit. 1919.
Stylosanthes guyanensis var. *intermedia* ssp. *anomala* Hass. in Fedde, loc. cit. 1919, ex char.
Stylosanthes guyanensis var. *subviscosa* f. *viscosissima* Hass. in Fedde, loc. cit. 1919. (T: *Hassler 6454*!)
Stylosanthes guyanensis var. *longiseta* (Micheli) Hass. in Fedde, loc. cit. 222. 1919.
Stylosanthes guyanensis var. *marginata* Hass. in Fedde, loc. cit. 223. 1919. (T: *Hassler 9938*!)
Stylosanthes ingrata Blake, in Proc. Biol. Soc. Wash. 39:51. 1928. (T: *Record s. n.*!)
Stylosanthes gracilis var. *vulgaris* Burkart, in Darwiniana 3:247. 1939, ex char.
Stylosanthes gracilis var. *subviscosa* (Benth.) Burkart, loc. cit. 248. 1939.

BRITISH WEST INDIES: TRINIDAD: St. Joseph savanna, *Britton, Hazen & Broadway 976* (GH, US, NY).

BRITISH HONDURAS: BELIZE: Belize, *Bartlett 11250* (US, NY). CAYO: Mt. Pine Ridge, *Bartlett 11706* (US, GH); Vaca Falls, *Record s. n.* (US). STANN CREEK: Stann Creek, *Schipp 486* (MO, GH, NY, F); Stann Creek, *Gentle 1883* (MO, GH, NY, F). TOLEDO: Swasey Branch, Monkey River, *Gentle 3898* (GH, F, US, NY, MO).

COSTA RICA: CARTAGO: Juan Viñas, *Rowlee & Stork 839* (NY, US). Cartago, *Léon 186* (F). HEREDIA: Santa Barbara, *Pittier 1656* (US). SAN JOSÉ: Santiago, *Brenes 14326* (GH, US); San José, *Tonduz 2169* (US, GH); El General, *Skutch 2462* (NY, US); San Pedro de la Calabaza, *Tonduz 10919* (US); Santa María, *Standley 41595* (US); between Aserrí and Tarbaca, *Standley 34031* (US). WITHOUT PRECISE LOCALITY: Boruca, *Tonduz 4707* (US); Río Colorado, *Valerio 278* (F).

EL SALVADOR: LA LIBERTAD: between Finca Germania and Finca San Antonio, near Comasagua, *Carlson 250* (F). SAN SALVADOR: from San Martín to Laguna de Ilopango, *Standley 22523* (US, NY); exact locality unknown, *Calderón 1133* (US, NY), *1287* (GH, US, NY); *Standley 19398* (NY, GH, US), *Velasco 8963, 8995* (US). SANTA ANA: vicinity of Metapan, *Standley & Padilla 3098* (F), *3261* (F). SAN VICENTE: San Vicente, *Standley 21318* (US, GH, NY).

GUATEMALA: ALTA VERAPAZ: Coban, *Standley 70111* (NY, F); Coban, *von Türckheim 84* (US). CHIMALTENANGO: Alameda, *Johnston 346* (F); from Chimaltenango to San Martín Jilotepeque, *Standley 57982* (GH, NY, F); San Martín Jilotepeque, *Standley 64402* (NY, F); San Juan-Malagua, *Johnston 1555* (F). CHIQUIMULA: El Rincón, *Standley 74734* (F). ESCUINTLA: along Río Guacalate, *Standley 89369* (F), *58200* (F); Finca El Zapote, *Muenscher 12417* (F); near Escuintla, *Standley 63577* (GH, F). GUATEMALA: Finca Bretaña, between Guatemala and Fiscal, *Standley 59690* (F); near Finca La Aurora, *Aguilar 18* (F); Chilloní, *Rojas 47* (US); exact locality unknown, *Salas 529*

(US). HUEHUETENANGO: along Río Cuilco, between Cuilco and San Juan, *Steyermark 50838* (F); Río Pucal, *Standley 65833* (F); east of San Rafael Pétzal, *Standley 83051* (F), *83076* (F); 14 miles south of Huehuetenango, *Standley 82398* (F). IZABAL: between Los Amates and Izabal, *Kellermann 7556* (NY, F), *7257* (NY, F); between Milla and Cristina, *Steyermark 38355* (F), *38653* (F); Gualán, *Blake 7691* (US); Cristina, *Blake 7585* (US); Quiriguá, *Standley 24223* (GH, US); near Quiriguá, *Standley 72470* (F). JALAPA: vicinity of Jalapa, *Standley 76661* (F); northeast of Jalapa, *Standley 76803* (F). JUTIAPA: vicinity of Jutiapa, *Standley 75042, 75511* (F). QUEZALTENANGO: Colomba, *Skutch 2048* (US, GH, F). QUICHÉ: between Cotzal and San Francisco, *Sharp 45169* (F); exact locality unknown, *Aguilar 1490* (F). RETALHULEU: near Retalhuleu, *Standley 88622* (F). SACATEPÉQUEZ: Barranco Hondo, *Standley 60232* (GH, F); Santa María de Jesús, *Standley 59401* (GH, NY, F); Ciudad Vieja, *Tejada 273* (US); near Antigua, *Standley 61723* (F). SANTA ROSA: southeast of Barberena, *Standley 77879* (F); Buena Vista, *Heyde & Lux 3752* (F); La Vega, *Heyde & Lux 4457* (US, GH). SUCHITEPÉQUEZ: Finca Las Nubes, *Steyermark 35442* (F); Tinca Mocá, *Skutch 1463* (GH). ZACAPA: Sierra de las Minas, *Steyermark 29647* (F).

HONDURAS: CHOLUTECA: vicinity of San Marcos de Colón, *Standley 15706* (US). COMAYAGUA: Siguatepeque, *Standley 56264* (US, F); vicinity of Comayagua, *Standley & Chacón 5972* (F); El Achote, near Siguatepeque, *Standley 56148* (F). COPÁN: Hacienda Espiritu Sancto, *Blake s. n.* (US). MORAZÁN: El Zamorano, *Molina 61* (F, US); San Antonio del Oriente, *Rodríguez 668* (F), *687* (F); Piedra Parada, *Standley 11937* (F); near Joya Grande, *Standley & Molina 4466* (F); Guaimaca, *Molina 2906* (F). OLANCHO: from Catacamas to Loma Pelona, *Standley 18283* (F). EL PARAÍSO: Quebrada de Dantas, *Standley, Williams & Molina 1260* (F); Yuscarán, *Molina 1694* (F); west of Güinope, *Merrill & Williams 15713* (F); Manzaragua Road, *Williams & Molina 11484* (MO, GH, F); Ofo de Agua, *Williams & Molina 12027* (GH, F); Güinope, *Rodríguez 1678* (F). SANTA BÁRBARA: Los Dragos, *Standley & Lindelie 7405* (F).

MEXICO: CHIAPAS: exact locality unknown, *Doyle 144* (US). JALAPA: Hacienda de la Laguna, *Schiede 631* (NY). JALISCO: San Sebastian, *Nelson 4075* (US, GH). OAXACA: Jalapa, *Pringle 9174* (GH). PUEBLA: Metlatoyuca, *Goldman 57* (GH, US). VERACRUZ: Minatitlan, *Mell s. n.* (NY); Zacuapan, *Purpus 1888* (NY, MO, US, GH, F); Orizaba, *Botteri 152* (GH). WITHOUT PRECISE LOCALITY: Lodiego, *Palmer 1900* (NY, GH, US, F); Monte Cristo, *Matuda 1958* (US, NY, GH); Vallecitos, Montes de Oca, *Hinton 11456* (US).

NICARAGUA: GRANADA: near Granada, *Grant 756* (GH). JINOTEGA: San Rafael del Norte, *Miller & Griscom 66* (US); southwest of Jinotega, *Standley 9534* (F), *10082* (F), *10094* (F).

PANAMA: CANAL ZONE: Sosa Hill, Balboa, *Standley 26443* (US); between Fort Clayton and Corozal, *Standley 29159* (US); Summit, *Standley 30068* (US); along Las Cruces Trail, *Hunter & Allen 753* (GH, MO); Río Puente, *Dodge, Steyermark & Allen 16835* (GH); Empire to Mandinga, *Piper 5129* (US). CHIRIQUÍ: Volcancitos, *Terry 1264* (GH, US, MO, F); COCLÉ: Penonomé, *Williams 167* (US, NY), *148* (US, NY); Natá, *Allen 838* (GH, US, MO, NY). PANAMÁ: Sabanaz, *Standley 25837* (US); Taboga Island, *Standley 28013* (US); between Matías Hernández and Juan Díaz, *Standley 32077* (US); Chêpo, *Hunter & Allen 75* (MO, GH); Pacora, *Bro. Maurice 790* (US).

ARGENTINA: CÓRDOBA: Sierra Chicas, Estancia la Reduccíon, *Burkart 7397* (F). CORRIENTES: Estancia, Santa Teresa, *Pedersen 79* (US). MISSIONES: Santa Ana, *Rodríguez 756* (MO); Posadas, *Ekman 1742* (NY); San Ignacio, *Ekman 1740* (US).

BOLIVIA: LA PAZ: Guanai-Tipuani, *Bang 1459* (MO, US, GH, NY, F); Nord Yungas, Coripata, *Büchtien 8101* (US, NY); Tipuani, *Büchtien 5423* (US, GH, MO, NY, F); South Yungas, San Bartolomé, near Calisaya, *Krukoff 10536* (US, MO, NY, F); Tampa, *Büchtien 1787* (US); La Joya, *Tate 1031* (NY); Mapiri, *Tate 466* (NY), *471* (NY); near La Paz, *Rusby 1008* (NY); Guanai, *Rusby 2324* (NY). SANTA CRUZ: Velasco, *Kuntze s. n.* (NY, US, F); Sará, Buena Vista, *Steinbach 6916* (GH, NY, F, MO); San José, *Williams 384* (US). WITHOUT PRECISE LOCALITY: Eskia, *White 612* (NY).

BRAZIL: BAÍA: Mucugé, Serra Sincorá, *Froes 20128* (NY). CEARÁ: Lagoa Porangaba, Fortaleza, *Drouet 2726* (GH, US, F). DISTRITO FEDERAL: Praía de Sernambetiba, *L. B. Smith 6359* (US). GOIÁS: Corgo do Jaraguá, *Pohl 949* (NY); Quexada, *Maceil 2132* (MO). MINAS GERAES: São Sebastião do Paraíso, *Vidal 3659* (GH); Caldas, *Regnell III428* (US); Uberaba, *Regnell 430* (US); Ilheos, *Moricand s. n.* (GH); Viçosa, *Mexia 4523* (NY, GH, US, MO, F); near Lagôa Pampulha, *Williams & Assis 6084* (GH); Estacão de Barreiro, *Williams & Assis 7122* (GH); Belo Horizonte, *Williams & Assis 5832* (GH, US); Bento Pires, *Williams & Moreira 5219* (GH); Tijuco, *Riedel 1316* (US); Canga, *Magalhaes 1760* (US); Engenho Nogueira, *Magalhaes 3168* (US); Santa Luzia, Chapeu de Sol, *Archer & Barreto 5015* (US); Jaboticatubas, *L. B. Smith 7078* (US); Diamantina, *Archer 4084* (US); Serra do Taquaril, *Barreto 5771* (F); Ituiutaba, *Macedo 1670* (US). PARÁ: Vigia, Campina do Palha, *Pires 4083* (NY); Gurupá, *Ducke 16182* (US); Colares, *Poeppig 2930* (NY); Belém, *Baldwin 4557* (US). PARAÍBA: Areia, *de Moraes 885* (NY). PARANÁ: Villa Velha, *Dusén 14781* (GH, F); Morungaba, *Dusén 16568* (GH); Tibagy, *Reiss 75a* (NY, F); Jaguariaiva, *Dusén 16381* (GH), *16596* (MO). PERNAMBUCO: Tapera, *Pickel 2403* (US). RIO DE JANEIRO: Cabo Frio, *Rose & Russell 20693* (US); Tijuca, *Riedel 1256* (US). SÃO PÁULO: Butantan, *Hoehne 137* (NY, GH); Iparanga, *Luederwaldt 13323* (NY); Capivari, *Riedel 1316* (US). WITHOUT PRECISE LOCALITY: Serra do Cipo, Conceicao, *Barreto 8994* (F); Rio Claro and Poracutu, *Pohl 2107* (NY); Socaja, *Mikan s. n.* (NY); Corrego Padre, *Pohl 1997* (NY, F).

BRITISH GUIANA: Pirara, *Schomburgk 381* (US); basin of Rupununi River, near mouth of Charwair Creek, *A. C. Smith 2376* (MO, NY, US, F); Orealla savanna, Berbice, *Irwin 330* (US); exact locality unknown, *Schomburgk 240* (US).

COLOMBIA: ANTIOQUÍA: Hayo Rico, *Correa & Barkley 18A200* (US); Medellín, *Archer 644* (US); Bello, *Archer 436* (US); San Antonio, *Bro. Daniel 530* (US, F); Fredonia, *Bro. Tomas 957* (US); El Prado, *Bro. Tomas 1009* (US); El Carmen, *Bro. Daniel 2310* (US). BOGOTÁ: Caqueza, *Traina 4327* (US). BOYACÁ: Mt. Chepon, *Lawrence 332* (NY, GH, F). CAUCA: Popayán, *Lehmann 2855* (US); El Tambo, *von Sneidern 1414* (NY, US); Albán, San José, *Arbeláez 2382* (US); Valle del Cauca, *Traina 4323* (NY); La Paila, *Holton 955* (NY); Cuatro Esquinas, *Pennell & Killip 6352* (US, NY). CUNDINAMARCA: La Esperanza, *Cuatrecasas 2472* (US); San Francisco, *García-Barriga 10981* (US); Estación Santana, *Dugand & Jaramillo 3831* (US, NY); Sasaima, *Bro. Ricardo s. n.* (US); Quetame, *André 1113* (F); Soncha, *André 1474* (F). HUILA: east of Neiva, *Rusby & Pennell 1111* (NY); San Augustín, *Bro. Daniel 4127* (US, F). MAGDALENA: Pueblo Bello, Valle Dupar, *Bro. Angel 673* (US); Santa Marta, Jordan, *H. H. Smith 58* (US, NY, GH, F); Jagua, *Allen 688* (MO). META: Cabuyaro, *Sprague s. n.* (US); Las Lagartija, southwest of Uribe, *Fosberg 19414* (US); Villavicencio, *Bro. Apollinaire s. n.* (US); El Mico airstrip, *Philipson, Idrobo & Fernandez 1310* (US). NORTE DE SANTANDER: del Sarare, Río Cubucón, *Cuatrecasas 18608* (US, F). SANTANDER: Río Casanare, Esmeralda, Los Llanos, *Cuatrecasas 3824a* (F). TOLIMA: Libano, *Pennell 3351* (NY); west of San Lorenzo, *Pennell 3491* (NY, US, GH); Mariquita, *Pennell 3673* (US, NY, GH). EL VALLE: Samaria, on Río Timba, near Timba, *Fosberg 20518* (NY, US); Las Neives, west of Cali, *Killip, Cuatrecasas & Dryander 39200* (US, F); Pavas, *Pennell 5505* (NY, GH), *5532* (GH, US); Dagua, *Arbeláez 3015* (US); east of Zarzal, *Pennell, Killip & Hazen 8461* (GH, NY, US); Santa Rosa, *Pennell & Killip 6073* (US, NY); Río Cali, Pichindé, *Duque 1650* (US); Cerro de Tres Cumbres, *Bermúdez & Barkley 17C845* (US); Cartago, Cuchilla de Santa Bárbara, *Cuatrecasas 22966* (US); El Forge, near Buenaventura, *Killip & Cuatrecasas 38938* (US, F). VAUPÉS: Río Guaviare, San José del Guaviare, *Cuatrecasas 7653a* (US). WITHOUT PRECISE LOCALITY: no location given, *Mutis 2345* (US), *2976* (US), *4683* (US).

ECUADOR: exact locality unknown, *Espinosa 590* (US).

FRENCH GUIANA: vicinity of Cayenne, *Broadway 709* (NY); west of Cayenne, *Cowan & Maguire 38013* (NY); exact locality unknown, *Bentham 20* (NY).

PARAGUAY: AMAMBAY: Sierra de Amambay, *Hassler 12043* (NY, F). CAAGUAZA: Yhú, *Hassler 9532* (NY, GH). CENTRAL: Cerros de Tobatí, *Hassler 6454* (GH, NY). LA CORDILLERA: Cordillera de Altos, *Fiebrig 405* (GH). SAN PEDRO: San Estanislão,

Hassler 6014 (GH, NY), *5996* (NY, GH), *7030* (NY, GH), *7081* (NY). WITHOUT PRECISE LOCALITY: Centurion, *Fiebrig 4397* (GH, US); Santa Elisa, *Hassler 2834* (MO, GH); Berghang, San Luis, *Fiebrig 4453-4413* (GH).

PERU: AYACUCHO: Aino, *Killip & Smith 22605* (NY, US). CUZCO: San Pedro, *Vargas 2576* (GH); Valle de Santa Ana, *Herrera 3614* (F). JUNÍN: Chanchosmayo Valley, *Schunke 1410, 1412, 1518* (F). SAN MARTÍN: near Moyobamba, *Klug 3638* (NY, GH, US, MO, F); Tarapoto, *Woytkowski 35097* (MO, F). TUMBES: La Palma, *Anderson 948* (US).

SURINAM: Republiek, *Kuyper 18* (US); Coppename River, Volksberg, *Pulle 279* (MO).

VENEZUELA: ANZOÁTEQUI: Los Caños, *Pittier 14472* (US); Río Cani, *Garroni 62* (US). BOLÍVAR: Gran Sabana, Hato Santo Teresa, *Tomayo 3202* (US); between Ciudad Bolívar and El Cristo, *Killip 37217* (US); Caño Piña, *Cardona 614* (US). COPEDES: San Carlos, *Rudd 331* (US). DISTRITO FEDERAL: Turmerito, *Killip 37138* (US, NY); Caracas, *Bailey & Bailey 97* (US); El Limón, *Williams 10540* (F). MÉRIDA: Tovar, *Fendler 297* (GH, MO); Montes de Zerpa, *Lossen 314* (US). MONAGAS: between Caripe and San Augustín, *Steyermark, 61783* (MO, F). TRUJILLO: Carretera Trujillo-Boconó, *Tomayo 1846* (US); Escuque, *Pittier 13150* (NY, MO, US). ZULIA: Mene Grande, *Pittier 10588* (US). WITHOUT PRECISE LOCALITY: Tobay, *Gehriger 358* (MO); Entrada, *Warming 100* (US).

Fig. 6

16b. STYLOSANTHES GUYANENSIS ssp. **dissitiflora** (Robins. & Seat.) Mohlenbrock, stat. nov.

Stylosanthes dissitiflora Robins. & Seat. in Proc. Am. Acad. 28:105. 1893. (T: *Robinson & Seaton 5172*!)
Stylosanthes purpurata Blake, in Proc. Biol. Soc. Wash. 33:52. 1920. (T: *Rose 2942*!)
Stylosanthes eciliata Blake, in Univ. Calif. Publ. Bot. 10:409. 1924. (T: *Purpus 9246*!)

MEXICO: JALISCO: near Guadalajara, *Rose & Painter 7478* (US, GH); southwest of Autlán, *McVaugh 14222* (US); near Etzatlán, *Rose & Painter 7543* (US, NY); Río Blanco near Guadalajara, *Pringle 11433* (US, GH); near Guadalajara, *Pringle 5172* (GH).

17. STYLOSANTHES ANGUSTIFOLIA Vog. in Linnaea 12:63. 1838, ex char. (T: *Sellow s. n.*)

Stylosanthes angustissima Klotzsch, in Schomburgk, Faun. Fl. Brit. Guin. 1200. 1840, ex char.
Astyposanthes angustifolia (Vog.) Herter, in Rev. Sudamer. Bot. 7:209. 1943.

Stems usually woody below, erect, much branched from the base, to 1 m. tall, slender, densely long-hispid or glabrescent. Leaflets linear to linear-lanceolate, acuminate, to 40 mm. long and 2.5 mm. broad, glabrous or rarely with scattered bristles on both surfaces, the margins often involute; petioles 2–16 mm. long, shortly bristly or nearly glabrous, the rhachis 1.5–3.5 mm. long; sheath of the stipules 3.5–7.0 mm. long, glabrous or usually with long tuberculate bristles and often villous, 5- to 9-nerved, the subulate teeth 2.5–4.5 mm. long. Spikes elongate, narrow, to 45 mm. long, 3- to 20-flowered; bracts unifoliolate, the leaflet often reduced to a small laminal projection, the sheath villous and usually with long bristles, 3–4 mm. long, 9- to 11-nerved, the teeth 2.0–3.5 mm. long; outer bracteole 1, 2.5–3.0 mm. long, ciliate near the apex; axis rudiment none; inner bracteole 1, 2.5–3.0 mm. long, ciliate. Calyx tube 3.5–5.0 mm. long, the lobes 1.5–2.5 mm. long and usually ciliate. Standard suborbiculate, 3.5–4.0 mm. long; wings 3–4 mm. long, auriculate at the base, shortly appendaged within; keel petals falcate, 1.5–2.5 mm. long, densely white hairy. Loment 0.8–1.5 mm. broad, 2–3 mm. long, faintly nerved, minutely pubescent, with only the small upper articulation fertile; beak 2.5–4.0 mm. long, strongly uncinate to circinate, usually over twice as long as the upper articulation.

Stylosanthes angustifolia seems to prefer low sandy areas in woods. It is known from British Guiana, French Guiana, Surinam, and northern Brazil (fig. 7).

BRAZIL: CEARÁ: margins of Açude Boa Agua, *Drouet 2422* (GH, F); Bairro do Tanape, Fortaleza, *Drouet 2366* (GH, NY, US, F). MARANHÃO: exact locality unknown, *Gardner 6000* (GH). PARÁ: Ilha do Mosqueiro, *Killip & Smith 30423* (NY, US); near Santarem, *Spruce s. n.* (GH, NY); exact locality unknown, *Tavares 13* (NY). PIAUÍ: exact locality unknown, *Gardner 2094* (NY). RIO BRANCO: Caracarahy, *Froes 23664* (NY); Surumu, *Ule 8161* (US). RIO GRANDE DO NORTE: Angicos, *Swallen 4715* (US). WITHOUT PRECISE LOCALITY: tropics, *Burchell 9004* (GH, NY).

BRITISH GUIANA: Roraima, *R. Schomburgk 536* (NY).

FRENCH GUIANA: Cayenne, *Rothery s. n.* (NY).

SURINAM: Wayombo River, *Linder 97* (GH, NY); Joden, *Kegel 1113A* (NY); Saron, *Kegel 1113B* (NY); Sectie Oeest, *Pulle 139* (US, MO); near Zanderij Island, *Archer 2813* (US); exact locality unknown, *Hostmann 1018* (NY, MO).

18. STYLOSANTHES LEIOCARPA Vog. in Linnaea 12:64. 1838. (T: *Sellow 4235*!)

Astyposanthes leiocarpa (Vog.) Herter, in Rev. Sudamer. Bot. 7:209. 1943.

Stems herbaceous to somewhat woody at the base, simple to much branched, ascending to suberect, nearly 0.5 m. tall, often viscid, densely and shortly bristly to glabrous near the base. Leaflets usually oblong, mucronulate at the apex, the terminal to 15 mm. long and 3 mm. broad, the lateral to 12 mm. long and 3 mm. broad, with short tuberculate-based bristles on both surfaces, with 2–4 pairs of very obscure veins not forming any submarginal nerve; petioles 3.5–4.5 mm. long, hispidulous, the rhachis 1.5–2.0 mm. long; stipular sheaths 4–6 mm. long, with 9–11 distinct veins, long-bristly, the subulate teeth 5–6 mm. long. Spikes 2.5–4.0 mm. long, 8- to 10-flowered; bracts unifoliolate, the leaflet hispid to short-bristly, the sheaths bristly, 3.5–4.5 mm. long with 7, rarely 9–11 veins, the teeth 2.5–3.5 mm. long; outer bracteole 1, 2.5–3.0 mm. long, ciliate near the tip; axis rudiment none; inner bracteole 1, 2.0–2.5 mm. long and ciliate. Calyx tube 2.5–3.0 mm. long, the lobes 2.0–2.5 mm. long and ciliate. Standard suborbiculate, 4–6 mm. long; wings 3.5–5.0 mm. long, auriculate, spurred within at the base; keel petals 3.5–4.5 mm. long, falcate. Loment reticulate with 1 or 2 additional longitudinal nerves besides the reticulate venation, about 2 mm. broad; both articulations fertile, or the upper sometimes abortive, or the lower abortive; upper articulation when fertile 2–3 mm. long and glabrous, the lower, when fertile, 1.5–3.5 mm. long and glabrous; beak somewhat uncinate or nearly straight, 2.0–2.5 mm. long, glabrous.

The species is known only through a few collections from Uruguay, Paraguay, southern Brazil, and southern Colombia. A specimen collected by Arsène from Morelia, Mexico, is obviously S. *leiocarpa*, but this extreme extension of the range seems unlikely. A note penciled on the sheet by S. F. Blake in 1924 states that this is "probably one of the sheets distributed by Otto Weigel and is badly mixed."

BRAZIL: MINAS GERAES: Osorio, Morro Grande, *Rambo S1747* (US). RIO GRANDE DO SUL: São Leopoldo, *Leite 1909* (GH); São João do Monte Negro, *Bornmüller 657* (GH). SANTA CATARINA: Palhoca Massiambú, *Reitz & Klein 653* (US).

PARAGUAY: exact locality unknown, *Hassler 7575* (NY).

URUGUAY: MONTEVIDEO: Pooitos/Carrasco, *Herter 76691* (GH, NY, MO, F); Montevideo, *Baratini s. n.* (MO); Carrasco, *Osten 6498* (US). SAN JOSÉ: Barra, *Herter 89069* (MO). WITHOUT PRECISE LOCALITY: Cabo Santa Maria, *Rosengurtt B2471* (NY).

19. STYLOSANTHES **cayennensis** Mohlenbrock, sp. nov.

Herba erecta ad 30 cm. alta caulibus parce ramosis glabris vel puberulis. Foliola elliptico-lanceolata supra glabra subtus punctulata puberula setosa nervis 4–6-gemmatis; foliolo terminali ad 12 mm. longo 3.5 mm. lato; petiolo 2–4 mm. longo glabro vel puberulo; rhachide 1–2 mm. longa; stipulae striatae vagina 3–6 mm. longa saepissime puberula processibus subulato-mucronatis setosis 3–5 mm. longis. Spicae densae oblongoideae floribus 3–10; bracteis plerumque unifoliolatis stipuliformibus vagina puberula vel setosa 3–6 mm. longa nervis 5; bracteola exteri-

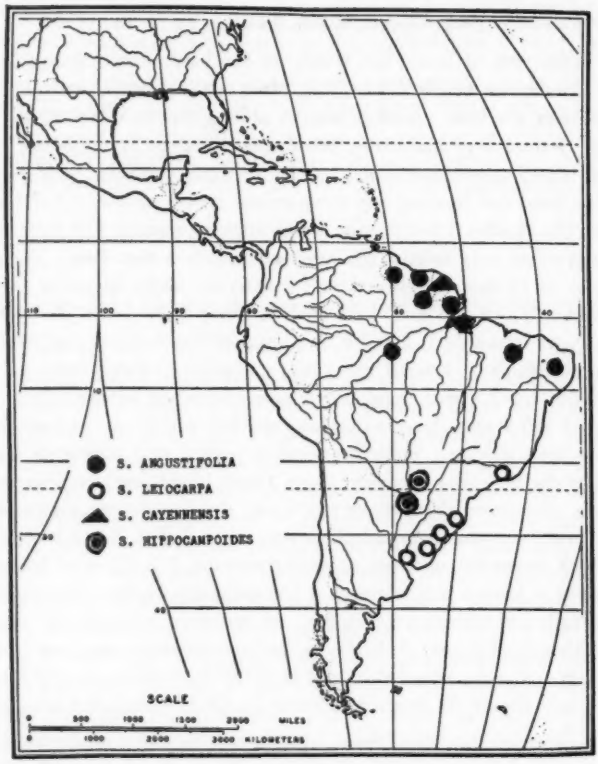

Fig. 7

ore 1, 2.5–3.0 mm. longa apice ciliata; axis rudimento nullo; bracteola interiore 1, 2.5–3.0 mm. longa apice ciliata. Calycis tubus 3.5–5.0 mm. longus glaber lobis 1.5–2.5 mm. longis. Corolla lutea; vexillo suborbiculato 4–5 mm. longo; alis falcatis 3.5–4.0 mm. longis; carina falcata 3.5–4.0 mm. longa. Lomentum 1.5–2.0 mm. latum reticulatum, articulo superiore 2 mm. longo glabro vel raro puberulo, articulo inferiore 1.5–2.0 mm. longo glabro, rostro circa 1 mm. longo valde uncinato vel circinato glabro.

Known only from wet habitats in the vicinity of Cayenne, French Guiana. It is related to S. *guyanensis* because of the glabrous loments and the short strongly uncinate beak but differs in its bi-articulate loments.

FRENCH GUIANA: vicinity of Cayenne, *Broadway 231* (US, NY, GH), *672* (NY, GH), *972* (GH, HOLOTYPE).

20. STYLOSANTHES **hippocampoides** Mohlenbrock, sp. nov.

Herba erecta ad 60 cm. alta caulibus parce ramosis setosis. Foliola linearilanceolata supra setosula subtus setosa nervis 3–4-gemmatis; foliolo terminali ad 15 mm. longo 2.5 mm. lato; foliolis lateralibus ad 15 mm. longis 2 mm. latis; petiolo 2–4 mm. longo puberulo vel setosulo; rhachide circa 1 mm. longa; stipulae striatae vagina 3–8 mm. longa glabra vel setosula processibus subulatis mucronatis setosis 3–5 mm. longis. Spicae densae ovatae floribus 2–6; bracteis plerumque unifoliolatis stipuliformibus vagina setosa 3–6 mm. longa; bracteola exteriore 1, 2–3 mm. longa apice ciliata; axis rudimento nullo; bracteola interiore 1, 2.0–2.5 mm. longa, apice ciliata. Calycis tubus 3.0–5.5 mm. longus glaber lobis 1.5–3.0 mm. longis. Corolla lutea; vexillo suborbiculato 3.5–5.5 mm. longo; alis falcatis 3–4 mm. longis; carina falcata 3.0–3.5 mm. longa. Lomentum circa 2 mm. latum valde reticulatum, articulo superiore 2.5–3.0 mm. longo glabro, articulo inferiore abortivo, rostro 2 mm. longo uncinato glabro.

Stylosanthes hippocampoides closely resembles S. *montevidensis* and S. *macrosoma*. *Stylosanthes hippocampoides* has conspicuously reticulate, glabrous loments about as broad as long and a 4- to 8-flowered inflorescence; *Stylosanthes macrosoma* has obscurely nerved, glabrous loments about twice as long as broad and a 2- to 6-flowered inflorescence; *Stylosanthes montevidensis* has a reticulate-nerved, pubescent loment about as broad as long and a 4- to 40- flowered inflorescence. The specific epithet is derived from the loment which superficially is shaped like the sea-horse (*Hippocampus*).

The species is infrequent in Uruguay and northern Argentina. Some specimens were included by Burkart in his S. *gracilis* var. *rostrata*. The presence of a distinct beak on the loment clearly distinguishes this species from S. *gracilis* of Burkart.

ARGENTINA: CÓRDOBA: Unquillo, *Cabrera s. n.* (F); Sierra Chica, *Kurtz s. n.* (NY); Sierra Achala, *Kurtz 8303* (NY, HOLOTYPE); Potrera de Loza, *Galander s. n.* (NY). CORRIENTES: Ituzaingo, Puerte Loreto, *Schuranz s. n.* (US); exact locality unknown, *Burkart 6743* (GH). MISIONES: Concepción, *Clos 2023* (GH).

URUGUAY: COLÓNIA: Riachuelo, *Herter 15562* (GH, US, NY, MO, F); exact locality unknown, *Clos 3231* (GH).

21. STYLOSANTHES MACROSOMA Blake, in Proc. Biol. Soc. Wash. 33:52. 1920. (T: *Morong 255*!)

Stylosanthes montevidensis f. *arenosa* Hass. in Fedde, Rep. Sp. Nov. 16:223. 1919, ex char.

Stems ligneous near the base, erect, branched, to 2 dm. tall, with soft white pubescence and some scattered tuberculate bristles. Leaflets narrowly elliptic, mucronate, acute, nearly glabrous above but with scattered bristles beneath, with 3–4 pairs of conspicuous veins forming a submarginal nerve; terminal leaflet to 14 mm. long and 2.5 mm. broad; petioles 3–5 mm. long, with scattered short bristles, the rhachis 1 mm. long or less; sheath of the stipules 4.5–5.5 mm. long, with scattered bristles, 11- to 15-nerved, the subulate teeth 3–4 mm. long. Spikes oblongoid to ovoid, 2- to 4-flowered; bracts unifoliolate, the leaflet 4–7 mm. long,

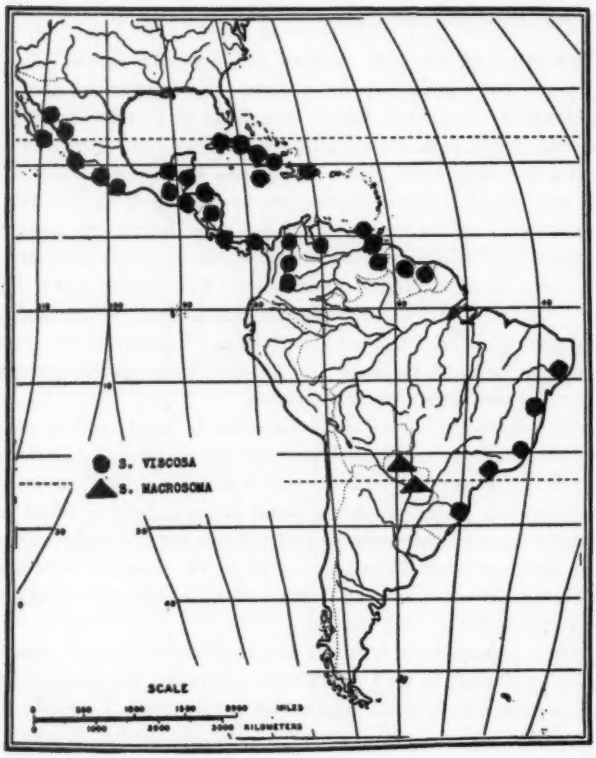

Fig. 8

the sheath 2.5–3.5 mm. long, 4.0 mm. broad, with scattered bristles and about 9 nerves, the teeth 3.5–4.0 mm. long; outer bracteole 3.0–3.5 mm. long, ciliate at the apex; axis rudiment none; inner bracteole 1, 1.0–2.5 mm. long, ciliate at the apex. Calyx tube 2.5–3.5 mm. long, the lobes 2–3 mm. long and ciliate. Standard suborbiculate, 4–5 mm. long; wings 3.5–4.5 mm. long, obovate, auriculate at the base and shortly appendaged within; keel petals 3–4 mm. long, subrostrate. Loment 2.0–2.5 mm. broad, weakly nerved; only the upper articulation of the loment fertile, 3.5–5.0 mm. long, glabrous except for some short hairs on the margin near the summit; beak strongly uncinate to nearly coiled, 1.5–2.5 mm. long, less than half as long as the upper articulation.

The type was distributed as S. *guyanensis* although Morong noted on the collection label that it was not quite like other specimens of S. *guyanensis* which he had collected. Hassler named this species as a form of S. *montevidensis*.

PARAGUAY: ASUNCIÓN: exact locality unknown, *Morong 255* (US, MO, GH, NY). WITHOUT PRECISE LOCALITY: *Hassler 7606* (GH, NY).

22. STYLOSANTHES VISCOSA Sw. in Prod. Veg. Ind. Occ. 108. 1788, ex char.

Hedysarum hamatum β L. Syst. Nat. 10:1170. 1759, ex char.
Stylosanthes glutinosa HBK. Nov. Gen. et Sp. 6:507. 1823, ex char.
Stylosanthes viscosa β *acutifolia* Benth. in Mart. Fl. Bras. 15[1]:91. 1859, ex char.
Stylosanthes viscosa f. *typica* Hass. in Fedde, Rep. Sp. Nov. 16:220. 1919, ex char.
Stylosanthes prostrata M. E. Jones, in Contrib. West. Bot. 15:135. 1929. (T: *Jones 24002*!)

Stems ascending and spreading or prostrate and matted, much branched, to 1 m. long, densely pubescent with short viscid hairs. Leaflets to 25 mm. long, 5 mm. broad, usually much smaller, acute or obtuse, punctate beneath, shortly hairy or hispidulous, with 2–4 pairs of conspicuous veins; petioles 2.5–5.0 mm. long, hispidulous, viscid, the rhachis 1–2 mm. long; sheath of the stipules 3.5–5.5 mm. long, 1–2 mm. longer than the teeth, hispidulous and viscid on the back, 3- to 5-nerved. Spikes small, crowded, ovoid, 2-to 5-flowered; outer bracts usually trifoliolate, inner unifoliolate, the sheath equaling or slightly exceeding the teeth, hispidulous and viscid on the back, 5- to 7-nerved; outer bracteole 1, 2.5–3.0 mm. long, ciliate at the apex; axis rudiment none; inner bracteole 1, 2.5–3.0 mm. long, ciliate at the apex. Calyx tube 3–7 mm. long, glabrous to puberulent. Standard suborbiculate, 4–7 mm. long; wings 4–5 mm. long, auriculate, spurred within at the base; keel petals 3–4 mm. long, falcate. Loment to 2.5 mm. broad; only the upper articulation of the loment fertile, 2–4 mm. long, shortly hairy, reticulate-nerved; beak short, less than half as long as the upper articulation, usually about one-third to one-fourth as long, shortly hairy, strongly uncinate, often coiled.

Most specimens possess subacute or obtuse leaflets 5–15 mm. long. Some have acuminate leaflets 15–25 mm. long, and these have been segregated as var. *acutifolia*. This variation occurs throughout the entire range of the species, however, although most of the specimens with longer leaflets are found in the southern part of the range.

Stylosanthes prostrata of Baja California is merely a heavily viscid, prostrate form of *S. viscosa*.

Stylosanthes viscosa has been reported several times as an adventive along the western coast of Africa.

CUBA: CAMAGÜEY: Camagüey to Santa Ana, *Britton 1960* (NY, US); south of Sierra Cubitas, *Shafer 505* (NY). HABANA: Guanabacoa, *Baker 2930* (NY); Gran Sierra, *Clemente 2078* (NY); Loma de las Yatas, *Ekman 574* (US); Loma de la Juta, *Wilson & León 11643* (NY, US); exact locality unknown, *Taber 1930* (NY). LAS VILLAS: Santa Clara, vicinity of Sancti Spiritus, *Shafer 12120* (GH, NY, MO, US, F); 12 km. east of Cascajal, *Howard 5578* (GH), *85534* (GH, NY); Cienfuegos, *Combs 407* (GH, US, NY, MO, F); La Magdalena, Cayamas, *Baker 2503* (NY, US); Manacas, *Jack 8713* (NY). ORIENTE: El Cobre, *Britton, Cowell & Shafer 12866* (NY, MO, US); Guantanamo Bay, *Britton 1960* (NY, US); exact locality unknown, *Wright 122* (GH, NY, MO). WITHOUT PRECISE LOCALITY: *Linden s. n.* (NY).

DOMINICAN REPUBLIC: SANTIAGO: El Rubio, *Jimenez 1058* (US). SANTO DOMINGO: Monte Cristi, *Ekman 12633* (US).

JAMAICA: Two-Mile-Wood, St. Catherine, *Harris 12406* (GH, NY, MO, US, F); Lititz savana, *Harris 12899* (GH, NY, MO, US, F); Abbey Green, *Orcutt 2869* (US); Kingston, *Hansen 1897* (NY); Spring Hill, Portland, *Harris 6630* (NY, US, F).

El Salvador: near Chalchuapa, *Calderón 1008* (US, GH).

Guatemala: jalapa: between Monjos and Jalapa, *Steyermark 32209* (F). jutiapa: Cerro Colorado, *Standley 76183* (F).

Honduras: comayagua: vicinity of Comayagua, *Standley & Chacón 5385, 5403* (F); Siguatepeque, *Standley 5627S* (F, US). el cayo: exact locality unknown, *Gentle 2245* (GH, F). morazán: Las Mesas, *Swallen 10793* (US); west of Chaquito, near Río Yeguare, *Standley 22948* (US); San Antonio, *Rodríguez 667* (F). el paraíso: Quebrada de Dantas, *Standley, Williams & Molina 1289* (F); Yuscarán, *Molina 1658* (F).

Mexico: baja california: San José del Cabo, *Jones 24002* (GH, NY, MO, US, F), *27236* (GH, US); Todos Santos, *Jones 24769* (MO, NY, F); Cape San Lucas, *Rose 16364* (NY, US). chiapas: Hacienda Monserrate, *Purpus 9126* (US); between Tapana, Oaxaca, and Tomala, *Nelson 2945* (US), *2950* (US). colima: east side of Manzanillo Bay, *Ferris 6199* (US). guerrero: 4 miles north of Acapulco, *Barkley, Rowell & Westlund 30* (F); Acapulco, *Palmer 10* (GH, MO). jalisco: San Sebastian, northeast of Hacienda del Cura, *Mexia 1373* (GH, MO). sinaloa: Río Florido, *Dehesa 1525* (US); Santa Lucia Concordia, *Dehesa 1632* (US). sonora: Alamos, *Rose, Standley & Russell 12693* (GH, US, F); Alamos, Río Puerte, *Gentry 2934* (GH, MO, US, F). tabasco: Achotal, Balancán, *Matuda 3041* (F, NY), *3047* (NY, F). zacatecas: near San Juan Capistrano, *Rose 2467* (GH, US).

Nicaragua: Volcán El Viejo, *Oersted 4740* (F).

Panama: panamá: vicinity of San Carlos, *Allen 1143* (GH, US, MO, NY).

Bolivia: cochabamba: Ayopaya, Sailopata, *Cardena 3186* (F). without precise locality: São Yungas, *Büchtien 210* (US); Urupana, *White 942* (NY).

Brazil: baía: Mt. Peludo, *Curran 391* (GH, US, F); Machado Portela, *Rose & Russell 19956* (US); Ilha de Itaparica, *Pires 3421* (NY); Busca Vida, *Bondar 2598* (F). distrito federal: Ipanema, *Barreto 5600* (F). minas geraes: Lassance, Pirapora, *Cochran s. n.* (US); Tejuco, *Vauthier 163* (GH); Ilheos, *Riedel 211-212* (GH, US). pernambuco: Prazeres, *Pickel 980* (GH, US, NY); Tapera, *Pickel 186* (F). rio de janeiro: near Rio de Janeiro, *Burchell 4109* (GH), *1174* (GH, NY); Copacabana, *Glaziou 5817* (NY). santa catarina: Laguna, *Reitz & Klein 4677* (US). são paulo: Campiña, *Krug & Zagatto 2191* (US); Butantan, *Gehrt 25239* (NY).

British Guiana: Berbice (or Demerara) Co., *Abraham 89* (NY); exact locality unknown, *Schomburgk 178* (US, NY).

Colombia: cundinamarca: Melgar, *Pennell 3608* (GH, US, NY, F). huila: east of Neiva, *Rusby & Pennell 1083* (GH, US, NY), *1042* (NY). magdalena: Rincón Hondo, *Allen 405* (MO). santander: Lebrija, *Molina 376* (US). tolima: Doima, *Haught 2444* (MO, US, F, NY); Honda, *Pennell 3608* (GH, US, NY, MO).

Paraguay: la cordillera: Ypacaray, *Hassler 11576* (GH, US, NY, MO). without precise locality: between Río Apa and Río Aquidaban-mí, *Fiebrig 4384-4082* (GH, US).

Surinam: Zanderij Island, *Maguire & Stahel 23733* (NY, US, F); Sectie Oeest, *Stahel & Gonggrijp 523* (US); Corantijn River, *Rombouts 166* (NY).

Venezuela: bolívar: Island of Margarita, Pt. Mosquito, *Johnston 249* (GH); between Ciudad Bolívar and El Cristo, *Killip 37234* (US); between Upata and Río Caroní, *Steyermark 57563* (MO, F). nueva esparta: Cocke Island, *Johnston 6* (US, GH). trujillo: Loma de Moron, near Valera, *Pittier 10721* (GH, US, NY).

23. Stylosanthes **figueroae** Mohlenbrock, sp. nov.

Herba humistrata vel suberecta basi ramosissima ad 20 cm. longa caulibus glabris vel puberulis. Foliola elliptico-ovata puberula nervis 3–5-gemmatis; foliolo terminali ad 10 mm. longo 5 mm. lato; foliolis lateralibus ad 10 mm. longis; petiolo 1–3 mm. longo glabro vel puberulo; rhachide 0.5–1.5 mm. longa; stipulae striatae vagina 3–7 mm. longa glabra vel puberula processibus subulatis mucronatis 3–5 mm. longis. Spicae parvae oblongoideae floribus 2–7; bracteis plerumque uni-

foliolatis stipuliformibus vagina puberula 3–6 mm. longa nervis 3–7; bracteola exteriore 1, 2.5–4.0 mm. longa apice ciliata; axis rudimento nullo; bracteola interiore 1, 2.0–3.5 mm. longa apice ciliata. Calycis tubus 3.5–5.5 mm. longus glaber lobis 1.5–2.5 mm. longis. Corolla lutea; vexillo suborbiculato 4.0–5.5 mm. longo; alis falcatis 3.5–4.5 mm. longis; carina 3.5–4.5 mm. longa. Lomentum pubescens circa 2 mm. latum reticulatum; articulo superiore 2.5–3.0 mm. longo puberulo; articulo inferiore abortivo; rostro 2.0–2.5 mm. longo uncinato puberulo.

Stylosanthes figueroae is distinguished from other members of its section by the pubescent loments with only one fertile articulation. It most nearly resembles *S. humilis* from which it differs in having the beak of the loment one-half to two-thirds the length of the upper articulation, rather than two to six times as long.

This species is known only from the vicinity of Cali, Colombia.

COLOMBIA: CAUCA: Cali, *Figueroa 897* (US, HOLOTYPE); Cauca, *Triana s. n.* (NY).

24. STYLOSANTHES MONTEVIDENSIS Vog. in Linnaea 12:67. 1838. (T: *Sellow s.n.*!)

Stylosanthes juncea Micheli, in Mem. Soc. Phys. Genève 28:7. 1883, ex char.
Stylosanthes juncea var. *setosa* Chod. & Hass. in Bull. Herb. Boiss., ser. 2, 4:884. 1904, ex char.
Stylosanthes montevidensis var. *juncea* (Mich.) Hass. in Fedde, Rep. Sp. Nov. 16:223. 1919.
Stylosanthes montevidensis f. *glabrata* Hass. in Fedde, loc. cit. 1919. (T: *Hassler 2709*!)
Stylosanthes montevidensis f. *setosa* Hass. in Fedde, loc. cit. 1919, ex char.
Stylosanthes montevidensis f. *typica* Hass. in Fedde, loc. cit. 1919, ex char.
Stylosanthes linearis Blake, in Jour. Wash. Acad. Sci. 14:287. 1924. (T: *Jörgensen 2693*!)
Stylosanthes gracilis var. *rostrata* Burkart, in Darwiniana 3:251. 1939, ex char.
Stylosanthes montevidensis var. *heterophylla* Burk. loc. cit. 260. 1939, ex char. (T: *Dusén s. n.*)
Astyposanthes montevidensis (Vog.) Herter, in Rev. Sudamer. Bot. 7:210. 1943.

Stems usually erect, to 1 m. tall, slender to robust, simple or often sparsely branched, glabrous to puberulent above or rarely throughout, usually with scattered long bristles. Leaflets lanceolate to linear, acute and mucronulate, glabrous to shortly hairy or occasionally with bristles along the costa beneath, with 2–4 pairs of conspicuous veins forming a submarginal nerve; terminal leaflet to 4 cm. long and 3 mm. broad, the lateral ones to 3 cm. long and 2.5 mm. broad; petioles 2.5–7.0 mm. long, glabrous, hispidulous, or short-bristly, the rhachis about 1 mm. long; sheath of the stipules 5–11 mm. long, sparsely bristly or densely short-hairy or rarely glabrous and with 13–21 often conspicuous nerves, the subulate teeth 3.0–7.5 mm. long, averaging about 4 mm. shorter than the sheath. Spikes globose, very small and few-flowered to large and over 40-flowered; bracts unifoliolate, the leaflet 2–5 mm. long, the sheath 2.5–4.5 mm. long, 2.5–5.0 mm. broad, ciliate along the margins or occasionally with a few bristles near the apex, usually 7-nerved, the teeth 1–4 mm. long; outer bracteole 1, 3–4 mm. long, ciliate at the apex; axis rudiment none; inner bracteole 1, 2–3 mm. long, often bifid, ciliate at the apex. Calyx tube 2–5 mm. long, the lobes 2–3 mm. long. Standard suborbiculate, 4.0–6.5 mm. long; wings 3.5–5.0 mm. long, auriculate at the base; keel petals 3.5–4.5

mm. long, falcate. Loment 2–3 mm. broad, reticulate-nerved; only the upper articulation fertile, 3.0–5.5 mm. long, densely short hairy, at least near the apex; beak strongly uncinate, densely short hairy, 1.5–2.5 mm. long, one-half to one-third as long as the upper articulation.

The variability of the species is attested to by the many varieties and forms which have been proposed. Many of these are based on tenuous characters, and there is no line of demarcation separating any of them. Micheli proposed S. *juncea* as a new species on the basis of the stem usually 4 mm. or more in diameter as opposed to 2 mm. for S. *montevidensis*. Hassler divided the S. *montevidensis* complex into two forms of "typical" S. *montevidensis* and two forms of var. *juncea*, recognizing the latter as a variety, even though stating that it was merely a robust form.

Blake described S. *linearis* in § STYLOSANTHES because of the presence of an axis rudiment 0.3–0.8 mm. long. This character was not discovered in the present study of the type. Blake also noted the presence of 2 bractlets (= inner bracteoles), but there is actually only 1 deeply bifid inner bracteole.

The size of the inflorescence is exceedingly variable, specimens at one extreme having spikes 2- to 5-flowered while those at the other extreme have spikes over 40-flowered.

Stylosanthes montevidensis is recognized from other members of its section by the one fertile pubescent articulation with the circinate beak about one-half as long as the articulation.

A specimen collected by Calderón from El Salvador in all probability is adventive although the species does extend from Argentina to Colombia.

EL SALVADOR: near Chalchuapa, *Calderón 1051* (NY, US).

ARGENTINA: CHACO: Resistencia, Margarita Belen, *Aguilar 1163* (MO); Las Palmas, *Jörgensen 2693* (GH, US, MO). CÓRDOBA: Sierra Chico, *Lossen 173* (GH, MO, F). CORRIENTES: San Martín, La Cruz, *Ibarrola 1770* (US); Estancia, Santa Teresa, *Pedersen 111* (US); Empedrado, *Pedersen 908* (US). CRUZ ALTA: Campi Alegre, *Schreiter 4078* (F). JUJUY: Capital, Quebrada de Chañi, *Schreiter 11083* (GH). MISIONES: Candelaria, Garupa, *Bertoni 2382* (F); Apóstoles, *Clos 1911* (GH). SALTA: Guachipas, Alemania, *Venturi 9957* (GH, US, MO). SANTA FÉ: Reconquista F.C.S.F., *Burkart 5883* (GH). TUCUMÁN: Burruyaco, *Venturi 2616* (GH, US) Las Cejas, *Venturi 2117* (US); Campa Alegra, *Venturi s. n.* (US). WITHOUT PRECISE LOCALITY: Cafi, Cancillo, *Venturi 5992* (US); La Granja, *Ekman 1743* (NY, US, MO).

BOLIVIA: LA PAZ: La Paz, *Bang s. n.* (US). SANTA CRUZ: Sara, Buena Vista, *Steinbach 6922* (GH, MO, F), *5243* (GH), *3219* (F), *6614* (F).

BRAZIL: PARANÁ: Serrinka, *Dusén 16261* (GH), *13718* (NY, US). RIO GRANDE DO SUL: Porto Alegro, *Malme 726* (F). SANTA CATARINA: Sombrio, *Collector Unknown C1397* (GH). SÃO PAULO: Capital, *Pickel 5499* (US). WITHOUT PRECISE LOCALITY: Turnig, *Dusén 9147* (US).

COLOMBIA: META: San Martín, *Dryander 3038* (US).

PARAGUAY: CENTRAL: Caballero, *Morong 399* (NY, US, MO). PRESIDENTE HAYES: Santa Elisa, *Hassler 2709* (GH, MO). WITHOUT PRECISE LOCALITY: Estancia Primera, *Jörgensen 4817* (NY, US, MO, F); Coro de Altos, *Hassler 1798* (NY), *1799* (NY).

URUGUAY: CANALONES: Atlantida, *Rosengurtt B2830* (NY). CERRO LARGO: Río Negro, Palleros, *Rosengurtt B79* (NY). COLÓNIA: Arroyo de Pintos, Artilleros, near Puerto Platero, *Bartlett 21194* (GH). CONCEPCIÓN: Guinta del Colegio, *Lorentz s. n.* (US). SALTO: San Antonio, *Osten 5375* (US); San Antonio, *Rosengurtt B1070* (GH, F).

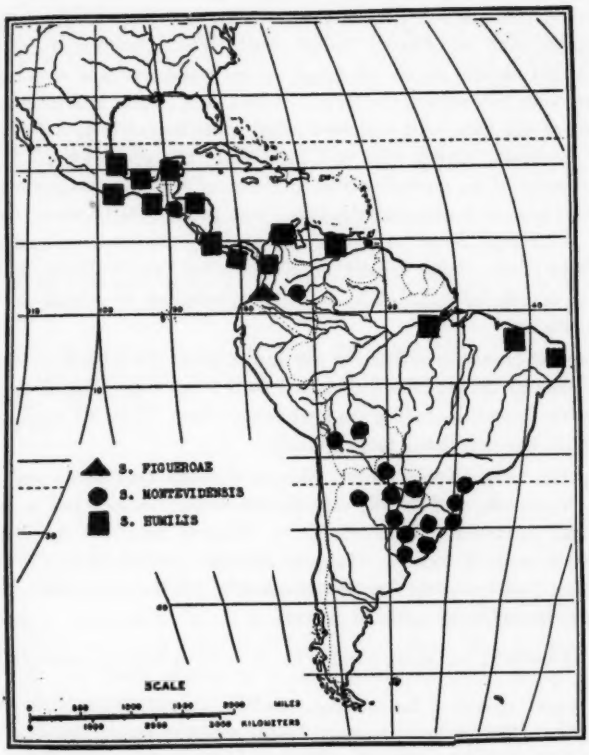

Fig. 9

25. STYLOSANTHES HUMILIS HBK. Nov. Gen. et Sp. 6:506. 1823, ex char.

Stylosanthes sundaica Taub. in Verh. Bot. Brand. 32:21. 1890, ex char.
Astyposanthes humilis (HBK.) Herter, in Rev. Sudamer. Bot. 7:209. 1943.

Stems usually ascending or sometimes prostrate, herbaceous to subligneous at the base, to 0.5 m. tall, branched, usually with short white hairs along one side of the stem, often with scattered short bristles, rarely nearly glabrous except near the base, the pubescence usually more dense immediately beneath each node. Leaflets lanceolate or sometimes elliptic, often mucronate, acute, short bristly-ciliate to nearly glabrous, with 3–4 pairs or usually conspicuous veins; terminal leaflet to 15 mm. long (rarely to 30 mm. long) and 3.5 mm. broad, the lateral ones to 11.5 mm. long and 3.0 mm. broad; petioles 2.5–5.0 mm. long, shortly hairy and often with scattered bristles, the rhachis 1–2 mm. long; sheath of the stipules 3–5 mm. long,

short-bristly and with 5–7 nerves, the teeth 2.5–3.5 mm. long, averaging about 1 mm. shorter than the sheath. Spikes short, ovoid, crowded, 3- to 4-flowered; bracts 1- to 3-foliolate, the sheath 2.5–4.5 mm. broad, nearly always bristly, rarely only ciliate, with 5–9 nerves, the teeth 2–3 mm. long; outer bracteole 2.5–3.0 mm. long, ciliate at the apex; axis rudiment none; inner bracteole 1, 2.0–2.5 mm. long, ciliate at the apex. Calyx tube 4–5 mm. long, the acute lobes 1.5 mm. long. Standard suborbiculate, spurred within at the base, 3–4 mm. long; wings 3–4 mm. long, clawed and auriculate at the base; keel petals 3.0–3.5 mm. long, falcate. Loment 1.5–2.5 mm. broad, reticulate-nerved; only the upper articulation fertile, 1.5–2.5 (–4.0) mm. long, usually only puberulent, rarely pilose; beak strongly uncinate to coiled, 1.5–3.5 (–5.5) mm. long, equaling to greatly surpassing the upper articulation.

Stylosanthes humilis is variable in size and shape of the leaflets and in size of the loments. Most specimens have leaflets less than 1 cm. long; others, to 3 cm. long. The size of the loment including the beak ranges from 3.5 to 9.0 mm. long. These differences are not correlated geographically.

The species ranges from central Mexico through Guatemala and Panama to Colombia, Venezuela, and Brazil; also occurs in the Antilles and is adventive in Malaysia and Australia. Specimens from Malaysia described by Taubert as *S. sundaica* are actually *S. humilis*. Taubert included *S. sundaica* in § STYLOSANTHES but with the axis rudiment "most caducous." In the specimens examined, no trace of an axis rudiment could be found.

CUBA: CAMAGÜEY: La Gloria, *Shafer 239* (NY). LAS VILLAS: Lomas de Bañao, *Luna 730* (NY).

EL SALVADOR: vicinity of San Salvador, *Standley 19399* (GH, US, NY).

GUATEMALA: CHIQUIMULA: between Zacapa and Chiquimula, *Standley 73693* (F); near Chiquimula, *Standley 73862* (F); north of Quezaltepeque, *Steyermark 31372* (US, F). ESCUINTLA: Río Guacalate, *Standley 58237* (NY, F). GUATEMALA: near Guatemala and Fiscal, *Standley 59788* (F). JALAPA: vicinity of Jalapa, *Standley 76411* (F). JUTIAPA: between Jutiapa and Plan de Urrutia, *Standley 75455, 74910, 75652* (F); between Agua Blanca and Amatillo, *Steyermark 30457* (F), *30450* (F). QUICHÉ: exact locality unknown, *Aguilar 1407* (F). SANTA ROSA: plains of Llano Entero, southeast of Chiquimulilla, *Standley 78796* (F); south of Guezacapan, *Standley 79431* (F); near Cuilapa, *Standley 77942* (F); Chupadero, *Heyde & Lux 4162* (GH, US). ZACAPA: vicinity of Zacapa, *Standley 74588, 73589* (F); between La Fragna and Estanzuela, *Steyermark 29126* (F).

HONDURAS: MORAZÁN: Río Yeguare, *Williams & Molina 16967* (GH, US, F); Agua Amarilla, *Williams & Molina 11027* (F); El Zamorano, *Rodríguez 1257, 2163* (F). EL PARAÍSO: exact locality unknown, *Standley 13600* (NY, US, F). YORO: near Progreso, *Standley 55048* (US, F).

MEXICO: CHIAPAS: Jalisco, *Purpus 9138* (US). COLIMA: Colima, *Palmer 108* (US). GUERRERO: Cutzamala, Cayuca, *Hinton 6985* (NY, US, F); Acapulco, *Palmer 25* (GH, US, NY, MO, F). JALISCO: Tecoman, *Orcutt 4447* (MO, GH, F); Barranca de Portillo, *Barnes & Land 240* (GH, US, F). MÉXICO: Temascaltepec, Tejupilco, *Hinton 1932* (US), *1931* (GH), *4767* (GH, US). MICHOACÁN: Apatzingán, Aguililla, *Hinton 5289* (US, GH, NY). OAXACA: San Gerónimo, *Mell 2117* (NY). VERA CRUZ: Acasonica, *Purpus 8894* (GH, US, MO); Zacuapán, *Purpus 2331* (GH, US, NY, MO, F); Minatitlán, *J. G. Smith 408* (MO).

PANAMA: CANAL ZONE: Corozal, *Standley 27403* (US); between Fort Clayton and Corozal, *Standley 29191* (US). COCLÉ: Aguadulce, *Pittier 4837* (US), *4983* (GH, NY, US). PANAMÁ: Las Sabanas, *Standley 41178* (US); near Panamá, *Standley 26794, 27730* (US); near Punta Paitilla, *Standley 26293* (US); between Panamá and Chêpo, *Dodge, Hunter, Steyermark & Allen 16700* (MO). VERAGUAS: west of Soná, *Allen 1054* (GH, US, MO).

BRAZIL: BAÍA: (data not legible) (MO). CEARÁ: Acude São Bento, Maranguape, *Drouet 2194* (GH, NY, MO, US, F). PARÁ: Boim, Rio Tapajoz, *Kuhlmann 18223* (US). PERNAMBUCO: Tapera, *Pickel 3036* (GH, US, F). RIO GRANDE DO NORTE: Angicos, *Swallen 4737* (US).

COLOMBIA: ANTIOQUIA: exact locality unknown, *Gutierrez, Klevens & Barkley 1463* (US).

VENEZUELA: GUARÍCO: between La Encrucijada and Misión Abajo, *Pittier 14925* (US); Mesa de El Sombrero, *Pittier 12489* (MO). MÉRIDA: near Tovar, *Fendler 1793* (GH, MO). TRUJILLO: Dividine, *Pittier 10823* (US). ZULIA: Maracaibo, *Pittier 10698* (NY, GH, US).

AUSTRALIA: QUEENSLAND: Townsville, *White 8818* (NY, US).

MALAYSIA: BALI: Tedjazolla, *deVoogd 2061* (GH). NOESA PENIDA: Sampelan near Tanglad, *deVoogd 2397* (GH).

JAVA: *Horsfield 91* (GH).

EXCLUDED OR DUBIOUS SPECIES

Stylosanthes rigida Spreng. Syst. 3:310. 1826. This species is described by a single phrase which could well apply to a number of species of *Stylosanthes*.

Stylosanthes tenuifolia G. Don, Gen. Syst. 2:281. 1832. Don distinguishes this species, which is known from the "Isle of Maranham, Brazil," by its narrow leaflets. While this likely applies to *S. angustifolia*, it could apply to narrow-leaflet forms of *S. guyanensis*.

Stylosanthes suborbiculata Chiov. Ann. di Bot. 13:381. 1915. The type for this species (*Paoli 239*), collected in 1913 in Somaliland, has not been seen and is therefore excluded from the systematic treatment. Chiovenda describes it as without an axis rudiment which distinguishes it from all other African species of *Stylosanthes* except *S. viscosa* which is adventive along the western coast of Africa. A photograph of *S. suborbiculata* may be found in Result. Sc. Miss. Stefan.-Paoli Somal. Ital. *t. 8* (1916) but this is of little value in determining the exact status of the species.

Stylosanthes rupestris Stuck. ex Seckt, Rev. Univ. Nac. Córdoba 17^{3-4}:145. 1930. This is a *nomen nudum* with only the location given by the author—Sierra (Malaguena), Argentina.

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Italicized numbers refer to collectors' numbers, *s. n. (sine numero)* to unnumbered collections; parenthetical numerals refer to the numbers assigned to the species in this monograph.

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